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Compiled by Hannah Grunseit

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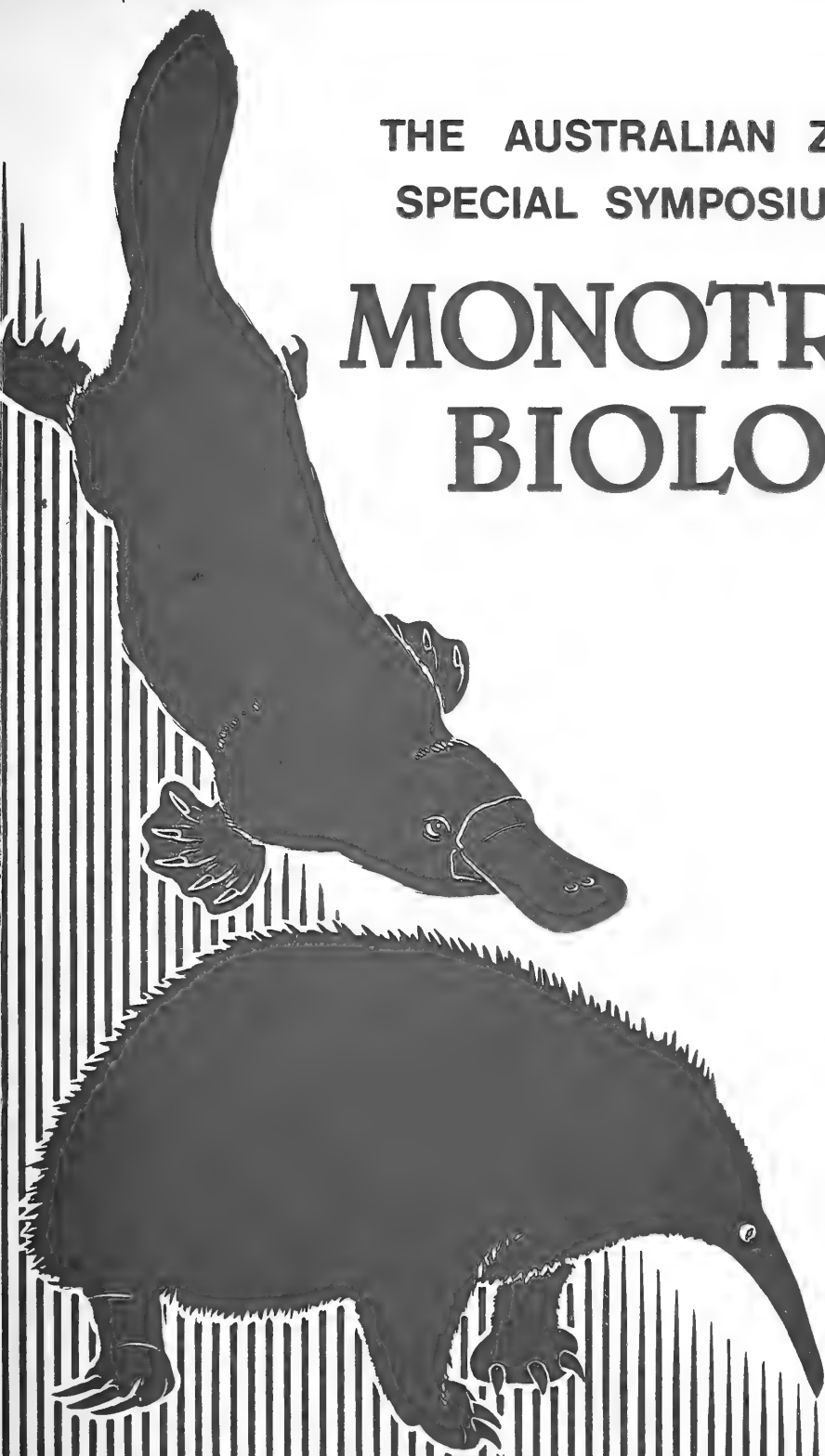
MONOTREME BIOLOGY

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VOL.20 PART 1



NOTICE TO AUTHORS

Papers will be considered for publication in *The Australian Zoologist* if they make an original contribution to whole animal biology of the Australian fauna. Papers submitted will be subjected to review and thence to the normal editorial process, in the course of which authors will receive edited galley proofs for correction. A manuscript is accepted on the understanding that it is to be published exclusively in *The Australian Zoologist*.

MANUSCRIPTS (original and one copy) should be sent to the Editor, "The Australian Zoologist", New South Wales State Fisheries, Fisheries House, 211 Kent St., Sydney, N.S.W. 2000. They should be typewritten (double spaced) on good quality paper. All pages of the manuscript must be numbered consecutively, including those containing references, tables and figure legends, which should all be placed after the text.

On the first page of the manuscript should appear the title of the paper, name of the author, the name of the Institution where the work was done and the present postal address if different from that of the Institution. Titles should be as brief, but as informative, as possible. A short title, to serve as a running head and consisting of not more than 50 letters (including spaces) must also be given on the title page.

The abstract (up to 200 words) should state concisely the scope of the work and the principal findings and should be suitable for direct use by abstracting journals. The section headings should be Introduction, Materials and Methods, Results, Discussion, Acknowledgements and References. Presentation must be clear and concise and all unnecessary repetition especially in consecutive sections should be avoided. Footnotes should be avoided.

REFERENCES are cited in the text by the author and date and are not numbered. Authors are referred to recent issues of *The Australian Zoologist* for the style used. No editorial responsibility can be taken for the accuracy of the references; authors are requested to check these with special care. Abbreviations of titles of periodicals should conform to those used in *World List of Scientific Periodicals*, 4th Edition.

TABLES should be numbered with arabic numerals, be accompanied by a title and be typed on separate sheets. Their approximate position in the text should be indicated by a note in the margin.

ILLUSTRATIONS AND DIAGRAMS should be larger than the size of the finished block. Drawings must not exceed 30 x 20 cm. If the originals exceed this they should be photographically reduced and good quality prints provided. Half tone prints should be arranged as plates and mounted on stiff white board up to a maximum size of 30 x 20 cm. Authors will be allowed up to two plates free of charge, but will be expected to pay the cost of any additional plates.

SHORT PAPERS these should be no more than six typewriter pages long and should deal with a technique experiment or important observation not reaching lengthy treatment. Isolated factual notes would not be considered suitable.

Monotreme Biology — Chairman's Summary of the Symposium

G. B. SHARMAN

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Hopson (1970) grouped all the nontherian mammals into a single subclass Prototheria. In Hopson's sense the monotremes are the only extant order of a diverse subclass of mammals (or quasi-mammals, see MacIntyre, 1967), so their ancestors are presumably to be found amongst one of the extinct prototherian orders. Mills (1971) considered that the living monotremes may have been derived from a *Morganucodon*-like ancestor, whereas Kermack and Kielan-Jaworowska (1971) favour derivation via the multituberculates. Earlier Simpson (1929) made a study of the vestigial molars of the platypus and concluded that the resemblance between these and triconodont teeth was "not very striking, but is at least as close as that between *Ornithorhynchus* and any mammals other than the triconodonts".

The discovery of undoubtedly monotreme teeth—the then only known remains of a Miocene monotreme called *Obdurodon insignis* (Woodburne and Tedford, 1975) aroused considerable interest. Although a great many millions of years have elapsed since Triassic times, when *Morganucodon* and the triconodont group disappeared from the fossil record, hopes were held that these Miocene monotreme teeth might be functional and might tell something about monotreme affinities.

Archer *et al.* (this Volume) have now found additional material—a dentary fragment and an ilium—presumed to belong to *Obdurodon*. The fossils are undoubtedly monotreme and are considered by the authors to be referable to the family Ornithorhynchidae. The ilium is from a young animal, but none-the-less indicates a less efficient burrowing habit than in the modern platypus. The dentary fragment may also be from a young animal and is edentulous, but the trough-like alveoli suggest that "*O. insignis* relied on the roots for stabilizing its molars, as do modern therians". If *O. insignis* had a bill it was probably not as well developed as in the modern platypus. The authors conclude that there is little chance of finding other types of monotremes at the poorly endowed sites from which known material came, so we must hold out hopes that other areas will eventually yield

the specimens so urgently required to evaluate the evolutionary relationships of the living prototherians.

Archer *et al.* (this Volume) believe that *Ornithorhynchus agilis* is conspecific with the living *O. anatinus*, so *Obdurodon* becomes the only fossil ornithorhynchid. Murray (this Volume) dealt with a number of fossils belonging to the tachyglossid family of monotremes. These underwent at least a minor adaptive radiation in Tasmania, mainland Australia and New Guinea, and some forms reached a size which justifies their inclusion amongst the Pleistocene megafauna. Whereas *Zaglossus* did not persist beyond the end of the last glaciation in Australia, the New Guinea species apparently survived by "following a narrow band of suitable habitat up and down the vertically zoned mountains".

In the absence of an interconnecting series of fossils we must rely on genetic, biochemical, physiological and anatomical data to evaluate the relationships between animal groups. Whittaker *et al.* (this Volume) present a masterly review of their extensive sequence studies on monotreme globins and they show that it certainly is not valid to assume, as some have done, that there has been a constant rate of mutation during the evolution of a particular protein. The estimates of dates of divergence based on different proteins are such that it is possible to assume, from α -haemoglobin data, that the monotremes diverged from the therian mammal line in late Triassic times and, from the myoglobin data, that divergence occurred as recently as the Cretaceous. Palaeontological and anatomical evidence does suggest divergence of therians from non-therians during late Triassic times while an essentially mammal-like reptile grade of organisation prevailed. However, Gregory (1947) suggested that the monotremes were degenerate or neotenuous marsupials and he grouped them with the marsupials in his subclass Marsupionta, a classification that few would accept today. A mid-Cretaceous origin of the monotremes would be in keeping with Gregory's hypothesis and that of Kühne (1973) but Whittaker *et al.* concluded that dates of divergence derived from their data did not support the concept of a constant rate of protein evolution and hence gave little information about times of divergence. What is now in doubt is the assumption of a constant rate of evolution for any protein and the entire hypothesis of the evolutionary "clock" based on protein data. The fundamental soundness of the sequencing data itself remains unchallenged.

Baldwin's paper (this Volume) is about adaptations of monotreme lactate dehydrogenase enzymes to temperature. His conclusions that "lactate dehydrogenases of monotremes have been finely tuned to operate under the specific thermal environment encountered" implies that this particular protein has been just as much subject to the effects of adaptation and natural selection as has any system or organ. Adaptive neutrality, the basis of the evolutionary "clock" hypothesis, cannot be assumed for lactate dehydrogenase.

The monotreme adrenal gland is anatomically unlike that of other mammals, but McDonald (this Volume) shows adrenocortical function to be essentially

CHAIRMAN SUMMARY

similar to that of other mammals. However, the echidna adrenal is the smallest, in relation to body mass, of all the mammals and its secretory rate is one hundredth that of "normal" mammals. It is thus not surprising to find that echidnas can survive adrenalectomy if not required to thermoregulate. The platypus has "mammalian size" adrenals, but is unique in another way—its major adrenocortical steroid is cortisone. Secretion rates of corticosteroids have not been measured in the platypus, but one platypus had plasma corticosteroid concentrations equivalent to those of therian mammals.

Essentially similar adrenocortical steroids are found throughout most of the vertebrates. However, Sernia (this Volume) shows that the steroid binding proteins of monotremes are rather different from those of other therian mammals, indicating a long separation of therian and non-therian stocks. Not surprisingly the steroid binding proteins of monotremes are generally unlike those of reptiles, but it is of interest that the monotremes appear to have retained a "fast" 17 β -estradiol binding protein (E_2 -SHBG) not found amongst therian mammals, but also retained in modern reptiles. As Sernia concludes, the retention of E_2 -SHBG in monotremes may be related to their "reptilian" mode of reproduction.

The literature on monotremes is enormous and few mammals have been so carefully investigated (Simpson, 1945). Simpson might have added that most of the investigations have been in the realm of comparative anatomy and that many of the papers are written in archaic German. One of Mervyn Griffiths' many valuable contributions was to provide a critical review of important earlier papers (Griffiths, 1968). Several contributors who already have, or intend to, publish elsewhere chose not to add to the monotreme literature and published their papers by title or abstract only. The abstracts appear at the end of this Volume.

Murtagh (1978) studied the chromosomes of all three extant genera of monotremes and found a chromosome system unique amongst mammals. All the monotremes have a chain of autosomes, present in single dose, appended to their sex chromosomes. In this, and in various other ways, the living species maintain a large amount of permanent chromosome structural heterozygosity. Murtagh's studies on the chromosomes show that the monotremes can hardly be neotenic marsupials as Gregory (1947) thought. She has also finally laid to rest an early assumption that the monotremes had chromosomes like some of the modern reptiles. Bohringer reported on that remarkable appendage, the bill of the platypus, which was first thought by European zoologists to be a hoax by some Antipodean taxidermist. Hers is an elegant study in neurophysiological mapping which shows large regions of the central nervous system devoted to inputs from the bill. Pridmore's studies of locomotion suggest that the monotremes employ a lateral thrust method of burrowing analogous to that employed by certain eutherian insectivores and that their locomotory methods are not primitive. A fossorial common ancestor for the three extant monotreme genera is suggested. Temple-Smith reports on the tubular alveolar gland which, coupled with the spur, gives the platypus the distinction of being one of the few known venomous mammals.

Metabolism in the long-beaked echidnas (*Zaglossus*) is typically like that of *Tachyglossus*, but the platypus has an elevated metabolism, more like that of therian mammals and presumably related to its thermally demanding environment (Dawson *et al.*, this Volume). The correlation between adrenal size and higher metabolic rate in the platypus would appear to be deserving of further study.

Tachyglossus is apparently monospecific and has a wider distribution in Australia and New Guinea than have most other indigenous, domestic or feral mammals. In Tasmania a markedly hairy form is found on 1,200 metre altitude plateaus, where it apparently survives under a metre or more of snow for extended periods. In central Australia and Arnhem Land a markedly spiny and almost hairless form thrives in areas of seasonal or non-seasonal extreme aridity, where air temperatures exceeding 40°C are commonplace. Augee (this Volume p. 105) has investigated the apparently clinal pelage variation in echidnas from Queensland, Victoria and Tasmania. Queensland echidnas did not respond to acclimation by growing hair, but metabolic differences between almost hairless and markedly hairy forms disappeared over a three-month period. Obviously short-term responses to fluctuating climatic conditions could be important in allowing the echidna to exploit a wide range of environmental conditions.

Flynn and Hill (1939) found a Tasmanian echidna with an intrauterine egg in late June and their latest uterine egg was found on September 4. Our own observations on spermatogenesis in Tasmanian echidnas are not complete, but active spermatogenesis does not occur in adult males during the warmer months of the year (October to March); it does occur in June and July, the coldest months of the year. During the period June 28 to July 8, 1978, five adult male echidnas were collected or examined in north-eastern Tasmania. All were active when found and one was taken at 1 a.m., when the air temperature was less than 5°C, at an altitude of about 80 metres. Numerous signs in the vicinity indicated that this echidna had been actively feeding prior to capture and later on the same morning frost extended to sea level. Maximum day temperatures during the collecting period were 11 to 15°C. As Augee (this Volume p. 111) points out, spermatogenesis (undoubtedly accompanied by mating, ovulation and embryogenesis) is unlikely to occur during periods of torpor or hibernation, which have not been demonstrated to occur in free-ranging echidnas even in southern latitudes. Regardless of whether the mammal-like reptiles were heterothermic or not, it seems that monotremes have achieved the ability to control their body temperatures by shivering thermogenesis, whereas the therians have specialised in non-shivering thermogenesis. Needless to say, Augee doubts the occurrence of hibernation in monotremes and believes that captive animals in which "torpor" has been observed were not in the best physiological condition. He concludes that the monotreme response to low ambient temperatures is tolerance, and to high ambient temperatures avoidance.

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None of the behaviour papers presented in this Volume are about avoidance behaviour in free-ranging monotremes, a topic which would be most difficult to study. In this context it is noteworthy that Augee *et al.* (this Volume) fail to confirm Brattstrom's (1973) observation of a loose hierarchy based on size in confined echidna populations. Brattstrom's pertinent remarks on evolutionary aspects of reptilian and echidna social behaviour are presented in abstract form in this Volume. Buchmann and Rhodes' studies (this Volume) on instrumental learning indicate a remarkable facility for improving performance and show the echidna to compare favourably with therian mammals tested in similar situations. It has long been known that monotremes (in common with marsupials) lack a corpus callosum, the dominant bond of nerve fibres connecting the two halves of the brain in eutherians. However, in spite of this, high levels of visual transfer between sides of the brain occur and the echidna eye is capable of accommodation in the apparent absence of intraocular muscles (Gates, this Volume).

Pirlot and Nelson's anatomical studies (this Volume) show that both echidna and platypus are comparatively well endowed in so far as brain and neocortical indices are concerned. These authors are, however, properly cautious about interpretation of their results, since they have no "basal" monotreme. Both monotremes compare very favourably with basal insectivores, and neocortical and cerebellar volumes of the platypus approach those of prosimians.

In view of the wide geographical distributions of both echidna and platypus, and the adaptation of echidnas to a variety of habitats, it is disappointing to find so few people working on monotreme ecology. The papers of Grant and Carrick (this Volume) on the platypus and of Augee *et al.* (1975) on the echidna are two of the few known to me. The platypus study was undertaken in an area already known to have a lot of animals, so population size is, perhaps, high compared to that prevailing elsewhere. None-the-less, a great number of comparable sites could be found in rivers from north Queensland to Tasmania, so the platypus can hardly be considered rare fauna. Perhaps ecological studies on monotremes are rarely done because of the immense amount of work involved in marking and following up large numbers of individuals which are "avoiders" in every sense of the word.

The Symposium heard three papers on the reproductive biology of monotremes. These papers were presented last, by which time the audience had learned that the many specialized adaptations found in monotremes hardly allowed them to be considered "primitive" mammals. However, Jones and Djakiew (this Volume) consider the primitive position for testes to be within the abdominal cavity—where monotremes keep theirs. Carrick and Hughes (this Volume) show both female and male reproductive systems to be very different from those of therian mammals. The significance of the cleidoic egg in mammalian evolution was discussed (Hughes and Carrick, this Volume), and here again the monotremes might be considered primitive for they, alone amongst the mammals, have large yolky eggs seg-

menting by meroblastic cleavage. However the monotreme egg is not cleidoic (closed) while in the uterus. Here, apparently under the influence of a well-developed corpus luteum of essentially mammalian structure, the bulk of the material used by the developing embryo is passed from uterus to egg through its shell. In many respects the monotremes might be regarded as marsupial ancestors in so far as reproduction is concerned. The monotreme neonate is hatched from the shell at about the same stage of development as prevails in the newborn marsupial, so a reduction in egg-yolk content and retention of the incubated phase of the monotreme egg in the uterus would give the marsupial condition. However Hughes and Carrick's paper warns us to beware of such generalisations—the so-called "yolk-bodies" eliminated from developing bandicott eggs are apparently not composed of yolk at all. Those, such as myself (Sharman, 1976), who have considered the "vestigial yolk body" of marsupial early cleavage stages as a reminder of ancestors with yolky eggs may be mistaken.

In general the theme of the Symposium was an evolutionary one. It was a useful gathering of experts and it highlighted those things about living and fossil monotremes that we do not know. The efforts (usually part-time) of a score or so of scientists have been directed towards understanding the biology of a small but enigmatic group of mammals—the sole survivors of the prototherian radiation. Why the monotremes survive millions of years after the extinction of their closest relatives remains a mystery. Perhaps the answer is threefold—monotremes have great intraspecies variability, unique adaptations to their environments, and are masters of avoidance behaviour. These three topics might be the theme of a future Monotreme Symposium.

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**Additional evidence for interpreting the Miocene
Obdurodon insignis Woodburne and Tedford, 1975,
to be a fossil platypus
(Ornithorhynchidae: Monotremata)
and a reconsideration of the status of
Ornithorhynchus agilis De Vis, 1885**

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ABSTRACT

More extensive excavations at the type locality of the middle Miocene *Obdurodon insignis* Woodburne and Tedford have produced a dentary fragment and an ilium apparently referable to *O. insignis*. The new specimens are clearly ornithorhynchid and corroborate the original familial assignment by Woodburne and Tedford (1975) made on the basis of isolated molars. The structure of the dentary fragment suggests *O. insignis* had at best a poorly-developed bill, but had other modifications concomitant with its evidently well-developed transversely shearing teeth. The ilium lacked the enlarged distal end characteristic of the modern platypus and presumably had smaller gluteus medius and iliacus muscles. These differences suggest the possibility that *O. insignis*, if it burrowed, may have done so less efficiently than the modern platypus. The new specimens do not appear to reveal autapomorphic characters that would demand placement of *O. insignis* on a collateral branch with, rather than on an ancestral lineage leading to, the modern platypus. They also do not appear to clarify broader questions about monotreme affinity because the features which differentiate them from the modern platypus, such as the better-developed alveoli, smaller mandibular canal and less expanded iliac head, are plesiomorphic features, and these are inadequate to indicate affinity to any other particular group of prototherian mammals.

Ornithorhynchus agilis De Vis, 1875, is placed in synonymy with the modern species *O. anatinus* (Shaw, 1792).

INTRODUCTION

In 1972 M. O. Woodburne and M. Archer obtained the holotype (SAM P18087) of *Obdurodon insignis* by screen-washing sands of the Etadunna Formation

at the locality known as SAM Quarry North (see Woodburne and Tedford, 1975), Lake Palankarina, Etadunna Station, South Australia. The paratype (AMNH 97228) had been collected by R. H. Tedford, T. H. and P. V. Rich, and R. T. Wells in 1971 from the locality known as South Prospect B (Woodburne and Tedford, 1975), Namba Formation, Lake Namba, Frome Downs Station, South Australia. In 1977 the present authors, with R. Brown, A. Kowanko and S. Van Dyck, quarried and screen-washed several tons of sand from SAM Quarry North. Not all of the resulting concentrate has been sorted, but results obtained so far include two specimens (Queensland Museum F9558 and F9559) that are clearly referable to *Obdurodon insignis* and considerably expand our knowledge of this most interesting animal.

Dental terminology follows Green (1937) and Woodburne and Tedford (1975), such that in the lower jaw the three ephemeral but functional teeth of the modern platypus are called M_1 , M_2 , and M_3 .

A DENTARY FRAGMENT REFERRED TO
OBDURODON INSIGNIS
(PLATES 1-2)

F9559 is the posterior part of a left dentary. It is missing the proximal end of the ascending ramus and the body of the dentary anterior to the alveoli for the second molar.

The alveolar region: The similar morphological and spacial configuration of the alveoli of F9558 compared with those in dentaries of the modern platypus suggest the tooth and root homologies shown in Plate 1. The M_3 is represented by one lingual alveolus that inclines posteroventrally, penetrating into the mandibular canal. The M_2 is represented by four distinct alveoli, two lingual and two buccal. The lingual pair are slightly advanced beyond the buccal pair. The postero-lingual alveolus of the M_2 is only just smaller than the other three, and all four penetrate into the mandibular canal. The M_1 is represented only by a remnant of a posterobuccal alveolus. This must have been comparable in development to the posterobuccal alveolus of M_2 . In the modern platypus each "alveolus" is represented by a conical depression, sometimes with a very small nutrient foramen at its base. These foramina are better developed in juveniles (e.g. J23753) than adults (e.g. J1086). Considering that the pelvic fragment described below and referred to *Obdurodon insignis* is from a young individual, there is at least a possibility that the very large size of the alveoli in the dentary fragment might also be in part a juvenile characteristic. However it is probable that the roots of the *Obdurodon insignis* molars (known to be well-developed in at least the upper posterior molar, Woodburne and Tedford, 1975) extended into these large alveoli, whereas in the modern platypus the meagre development of the roots suggests that the foramina in the alveoli only function to pass soft tissues rather than to

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also enclose roots. In *O. insignis*, therefore, the alveoli would probably have remained large as long as the animal retained its teeth.

There is another aspect of the alveoli of the *Obdurodon insignis* specimen that invites comment. In marsupials, at least, the roots of the lower molars themselves do not actually invade the mandibular canal, but are contained in a bony sheath that develops around the root and binds it principally to the lingual wall of the dentary. In *O. insignis* the alveoli, although steep-sided, are very shallow and no bony sheath extends into the mandibular canal. The alveoli open broadly and directly into the mandibular canal, suggesting either that the roots of the teeth were no longer than the very shallow depth of the alveoli, or that the ends of the roots freely projected into the mandibular canal. The roots of the holotype (an upper molar) are well-developed, but only just longer than the depth of the alveoli of the dentary. Therefore it is probable that the roots of the molars extended into the dentary no further than the open bases of the alveoli.

The alveolar area in *Obdurodon insignis* is trough-like and only gently recessed from the lingual and buccal alveolar rims. This contrasts with the much wider and deeper alveolar region of the modern platypus. This difference suggests that *O. insignis* relied on the roots for stabilizing its molars, as do modern therians. In the modern platypus the wide and deeply recessed alveolar region is probably necessary to help immobilize the shallow rootless horny pads.

There do not appear to be any low transverse ridges or septa in the alveolar area of *Obdurodon insignis*. Such ridges commonly (though not invariably) occur in the modern platypus, and the significance of their absence in *O. insignis* is not clear.

The masseteric fossa and mandibular canal: The masseteric fossa of *Obdurodon insignis* is wide and deep, as in the modern platypus. It differs only in that the anterior edge of the lateral rim of the fossa was more anteriorly situated and the posterior rim was more recumbent than in the modern platypus. The more anterior position of the masseteric fossa could be interpreted as an adaptation for obtaining greater leverage in chewing and a reflection of the better-developed teeth. The anterior end of the masseteric canal broadly connects to the mandibular canal via a masseteric foramen. In the modern platypus this foramen is very small and situated at the anterior tip of the masseteric fossa. In *O. insignis* the masseteric foramen occurs posterior to the anterior end of this fossa. The mandibular canal in *O. insignis* is subrounded in cross-section at the level of the posterior end of M₁. In the modern platypus it is larger and oval, being transversely wide.

The mandibular foramen: In *Obdurodon insignis* this foramen is small relative to the modern platypus and this is unexpected. With the information we presently have about *Obdurodon insignis*, such as the presence of well-developed teeth, it might be expected that requirements for innervation and vascularization of the

dentary would be at least as well-developed in the fossil as in the modern form. In the latter the mental foramen and anterior dental foramen combined almost equal the cross-sectional diameter of the mandibular foramen. This suggests that the vast majority of nerves and vessels passing through the mandibular canal serve the anterior region of the dentary and associated bill structures. The smaller size of the mandibular foramen (and in fact the mandibular canal) in *O. insignis* suggests the possibility that if it had a bill, it was not as well-developed as in the modern platypus.

The angular process: The angular process in *Obdurodon insignis*, which in most marsupials and some placentals gives attachment to the pterygoideus and masseteric muscles, is distinct although small. In most specimens of the modern platypus it is either absent or represented by a slight and diffuse thickening of the posteromedial ventral rim of the dentary. However, in some specimens (pers. comm. M. Griffiths) it is well-formed and sharp. Assuming that the distinct angular process in the fossil is characteristic of, rather than an abnormal occurrence in, *O. insignis*, this might be seen as an adjunct to the better-developed transversely shearing molars. Although an angular process is not developed in other prototherians, such as triconodonts or multituberculates, none of these have transversely shearing molars.

The internal coronoid process: This posteromedially projecting process is as well-developed in *Obdurodon insignis* as it is in the modern platypus. It differs in projecting posteroventrally rather than posterodorsally as it does in all specimens of the modern platypus observed. The significance of this difference is not understood.

AN ILIUM REFERRED TO *OBDURODON INSIGNIS* (PLATE 2)

F 9559 is an isolated left ilium missing only a part of the distal head of the bone. It is apparently juvenile because the posterior boundaries of this pelvic fragment are the undamaged ilium-ischium and ilium-pubis bone boundaries. Accordingly, only the anterior third of the acetabulum is represented.

Comparisons below are made with two juvenile platypuses (J23753, ilium maximum length 16.4 mm; J811, ilium maximum length 20.3 mm) and several adults (including J2414, ilium maximum length 26.4 mm).

The lateral face: The most marked difference between the juvenile ilium of *Obdurodon insignis* and juvenile, as well as adult, modern *Ornithorhynchus anatinus* ilia is the much more poorly developed distal iliac head of the first. Although there is some damage to the fossil, it clearly shows less distal expansion than even the most juvenile ilium of *O. anatinus* examined, and even less than the cartilagenous ilium of the 16 mm embryo illustrated by Low (1929: fig. 1).

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The muscles of the thigh of *Ornithorhynchus anatinus* have been reviewed by Pearson (1926) and her determinations of their homology are used here. Pearson's analysis was also corroborated by dissection of J9654. The principal muscles attaching to the ilium are shown in Figure 1. Of these, the largest are the gluteus medius (combined with the poorly differentiated gluteus minimus), which originates in the large dorsal gluteal fossa, and the iliacus, which originates from the large ventral iliac fossa. The gluteus medius inserts onto the greater trochanter of the femur and the crest immediately distal

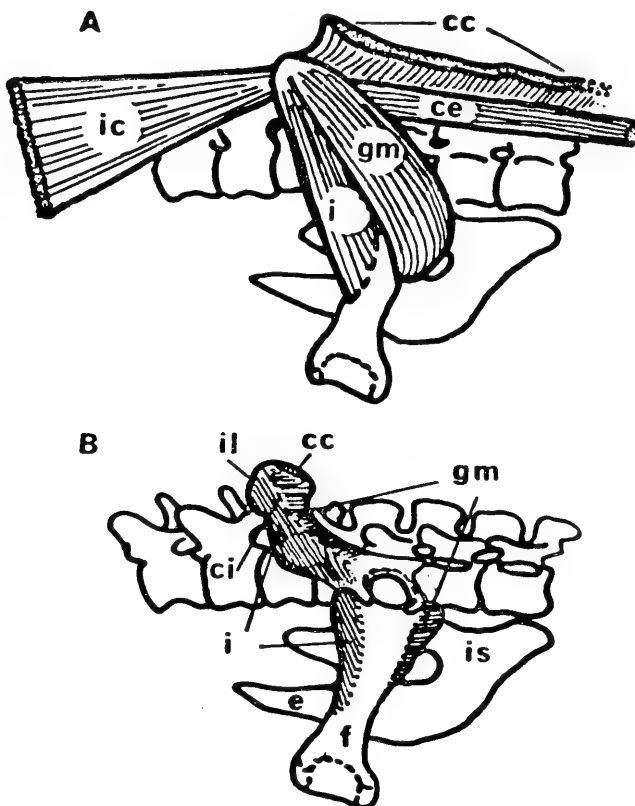


FIG. 1—A schematic portrayal of the principal muscles attaching to the distal half of the left ilium of a modern platypus, *Ornithorhynchus anatinus*. The musculature is based on J9654; the skeletal portrayal is modified after Pearson (1926). A, the muscles are shown intact except for the severed ilio-costalis, cruro-coccygeus, and the caudal extensor. B, the areas of muscle attachment are shown. Abbreviations: cc, cruro-coccygeus, or its area of attachment; ce, a caudal extensor; ci, crest of the ilium that divides the dorsal gluteal fossa from the ventral iliac fossa; e, epipubic bone; f, femur; gm, gluteus medius (and gluteus minimus), or its area of attachment; i, iliacus, or its area of attachment; ic, ilio-costalis; il, ilium; is, ischium.

to that process. Contraction of this muscle must rotate the femur, as well as draw the leg forwards. The iliacus (and psoas muscles, which are not clearly differentiable) inserts on the dorsal and anterior surfaces of the femur. Contraction of this muscle would also draw the leg forward.

Other muscles attaching to the dorsal surface of the iliac crest include the *cruro-coccygeus*, which has a small head originating on the iliac crest and an insertion by a tendon to the ankle. This muscle would flex or draw the leg backwards. There is a relatively large caudal extensor (see also Low, 1929, who illustrates this muscle) that attaches to the medial side of the iliac crest and inserts on to the neural arches of the caudal vertebrae. It would clearly be important in flexing the tail.

A very broad muscle originates from the anteroventral surface of the iliac head, near the symphysis with the anterior zygapophysis of the first sacral vertebra, and then radiates out to cover the rib cage. This is presumably the *ilio-costalis*, a part of the *erector spinae*. It is not one of the muscles reviewed by Pearson (1926), but is evidently the muscle identified as the *latissimus dorsi* by Manners-Smith (1894). Contraction of this muscle would flex the thorax relative to the pelvic girdle.

In the ilium referred here to *Obdurodon insignis*, the areas for attachment for all of these muscles are smaller than they are in the modern platypus, but most markedly so for the *gluteus medius* and the *iliacus*. Elftman (1929) points out that a well-developed *ilio-psoas* (*iliacus* plus the *psoas* muscles) is an important adaptation to a fossorial mammal (such as a wombat) in helping to keep the body from being pulled forward as the forelimbs dig. Similarly, the large size of the *gluteus medius* in the modern platypus might be an adaptation for the same purpose because in the platypus contraction of this muscle would also prohibit forward movement of the body if the hind limbs gripped the floor of the burrow. Therefore it is possible that *Obdurodon insignis* was a less efficient burrower than the modern platypus.

The lateral side of the ilium of the modern platypus is characterized by a very prominent and steep-sided iliac crest. This feature develops in prominence as a function of age, with very juvenile modern platypuses (e.g. J23753) entirely the crest. The subdued nature of such a crest in the evidently juvenile *Obdurodon insignis* ilium is therefore not surprising. However, adjacent to this incipient iliac crest extending from the posterior tip of the sacroiliac junction, parallel to the main iliac crest, and on to the head of the ilium. It could conceivably represent a boundary absent in the modern platypus between heads of the *gluteal* muscles. Whatever the reason, the result is that the two parallel iliac crests in *O. insignis* alter the standard primitive mammalian triangular cross-section of the ilium.

There is only a very slight depression for the *rectus femoris* muscle anterior to the edge of the acetabulum. This is also a juvenile character of the modern

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platypus and does not indicate any difference in the two forms. In adults this muscle produces a prominent scar on the iliac crest.

The medial face: Once again the most striking difference is the narrow distal head of the ilium in *Obdurodon insignis*. The medial surface of this head contacts the enlarged anterior zygapophysis of the first sacral vertebra. In *O. insignis*, as in living monotremes (Howes 1893: 544), there was a sacral arcade. This is a passage in the modern platypus bounded dorsally by the anterior zygapophysis of the first sacral vertebra, laterally by the ilium, ventrally by the transverse process of the first sacral vertebra, and medially by the neural arch of the same vertebra.

In the modern platypus the medial face of the iliac head bears not only the scar for the transverse process of the first sacral vertebra, but distal to this, it also exhibits a broad area for attachment of the ilio-costalis. The fossil ilium does not appear to have two discrete areas on the proportionately much smaller head. There is one distinct scar, and this is interpreted here to represent the area of future ankylosis with the prezygapophysis of the first caudal vertebra. It is most probable that an ilio-costalis attached near the distal end of the iliac head, as in the modern platypus, but it must have involved a much smaller and less conspicuous area than in the modern platypus.

The sacro-iliac area of attachment of the ilium of *Obdurodon insignis* is comparable in shape to that in the modern platypus and suggests that at least two vertebrae composed the sacrum.

Huxley (1879) and Howes (1893) document the ontogenetic changes in orientation of the ilium with respect to the sacrum along the "sacral axis". The ilium becomes more vertical with respect to the "sacral axis" as the platypus ages. In the ilium of *Obdurodon insignis*, the shape of the sacro-iliac symphysis suggests that the long axis of the ilium formed an angle of about 60 degrees with the horizontal "sacral axis". This is comparable to a sub-adult ontogenetic stage of the modern platypus.

DISCUSSION

There are several reasons why it seems reasonable to refer the fossil dentary fragment described above to *Obdurodon insignis*.

First there is the morphology of the dentary fragment. It is clearly most similar among known mammals to modern *Ornithorhynchus anatinus*. Woodburne and Tedford (1975) also conclude that the tooth representing the holotype is most similar to the molars of *O. anatinus*. These independent conclusions lend support to the suggestion that the fossil tooth and dentary are conspecific. The alveoli of the dentary fragment also indicate that it represents an animal whose teeth would be about the same size as the holotype of *O. insignis*.

Second, features in which the holotype differs from the modern platypus, are also features reflected in the dentary fragment, such as the long roots of the holotype and the well-developed alveoli of the dentary fragment.

Finally, despite several years of intensive screen-washing in the Miocene sites at Lake Palankarinna and Lake Namba, only two teeth of *Obdurodon insignis* have been found. Evidently it was either a rare animal in the Miocene of those areas, or relatively immune to fossilization. And, in contrast to the faunas from several adjacent sites, the fauna from the type locality at SAM Quarry North at Lake Palankarinna contains remarkably few mammals. It is the type locality for *Perikoala palankarinna* (one dentary fragment and several isolated molars), but otherwise has so far produced only a few isolated diprotodont molars. The possibility of finding a second ornithorhynchid at precisely the same otherwise extremely poorly-endowed site, and further that the second species was structurally and metrically comparable to the first, seems highly improbable.

Reference of the pelvic fragment to *Obdurodon insignis* is less certain but again probable. Because of its apparent possession of a sacral arcade it clearly resembles monotremes. Similarly, it is about the right size one would expect for an ilium of *O. insignis*. And perhaps most indicative, its steep orientation with respect to the sacrum is clearly an ornithorhynchid character.

This triangulation of similarity to *Ornithorhynchus anatinus* on the part of all three similarly sized specimens (molar, dentary and ilium) and their occurrence in an otherwise impoverished site are the main reasons involved in making the assumption that they are all referable to *Obdurodon insignis*.

The new specimens referred here to *Obdurodon insignis* corroborate the determination of Woodburne and Tedford (1975) that the original material represents an ornithorhynchid similar to but yet generically different from, *Ornithorhynchus anatinus*. The dentary fragment also corroborates their determination that the holotype is an upper rather than a lower molar because the roots of the holotype do not match the alveoli of the dentary fragment.

The mandibular canal of *Obdurodon insignis*, in being proportionately smaller than in the modern *Ornithorhynchus anatinus*, suggests *O. insignis* did not have as well-developed a rostrum as its modern relative. This presumably more primitive condition is also reflected in the pelvis which appears to lack the marked enlargement of the distal head of the ilium found in the modern form which suggests that *Obdurodon insignis* was not as efficient a burrower as *Ornithorhynchus anatinus*.

There are no obvious autapomorphic features in *Obdurodon insignis* that would prohibit this fossil form from being regarded as ancestral to, rather than on a collateral line with, the modern platypus. Many of the features that differentiate *O. insignis* from the modern platypus are clearly autapomorphic specialisations in the modern platypus. For example, the well-developed teeth and alveoli of

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O. insignis are almost certainly plesiomorphic character states secondarily reduced in the modern platypus. Similarly, the greater enlargement of the mandibular canal and lateral expansion of the head of the ilium in the modern platypus are features that could have evolved from the more ancestral condition found in *O. insignis*. Nevertheless, the possibility clearly remains that *O. insignis* was not ancestral to *Ornithorhynchus anatinus*.

When the teeth of *Obdurodon insignis* were first described, the morphology left little doubt about their ornithorhynchid nature. Discovery of the dentary and pelvic fragments from the type locality, their obviously close resemblance to the corresponding elements of the modern platypus, and well-developed condition of the alveoli of the dentary fragment now provide further justification for regarding the well-formed previously known fossil teeth to represent a more plesiomorphic ornithorhynchid condition.

There is nothing in particular about *Obdurodon insignis* that indicates any closer relationship to the other major group of monotremes, the echidnas, than exists already between the echidnas and the modern platypus. The points in which *O. insignis* differs from the modern platypus and yet appears to more closely approach the echidnas (i.e. the smaller mandibular canal and the less expanded head of the ilium) are probably simply primitive states in the evolution of the more modern ornithorhynchids rather than indicators of specific affinity with echidnas. The materials now known of the Miocene *O. insignis* can only be interpreted to indicate that it was morphologically almost as distinct from the modern echidnas as is the modern platypus.

Woodburne and Tedford (1975) consider the possible affinities of monotremes to other prototherians on the basis of the teeth of *Obdurodon insignis*, but find no close resemblance to any other known prototherian group. The structure of the dentary and the pelvic fragment similarly do not indicate any particular affinities to one or another of the prototherian groups although in the simple construction of the head of the ilium, *O. insignis* departs much less from the primitive form seen in some triconodonts (e.g. *Eozostrodon* and *Erythrotherium*, Jenkins and Parrington 1976) than does the modern platypus. However, in the steep inclination of the ilium with respect to the sacral axis, *O. insignis* is decidedly platypus-like. The dentary fragment of *O. insignis* has a small but distinct angular process and in this regard approaches several other prototherian (as well as metatherian) groups, but in its lack of any trace of post-dentary elements (or grooves for them), such as the splenial, it is decidedly unlike the same triconodonts noted above (Parrington 1971).

Mills (1971) suggests monotremes may have been derived from morganucodontid triconodonts on the basis of the dentition of *Ornithorhynchus anatinus*, but Woodburne and Tedford (1975) consider that the modifications required to transform the longitudinally shearing morganucodontid molars into the transverse shearing dilambdodont molars of ornithorhynchids are radical.

Basicranial morphology suggests to Kielan-Jaworowska (1971) and Kermack and Kielan-Jaworowska (1971) that monotremes are related to multituberculates. *Obdurodon insignis* is not yet represented by any basicranial material.

THE STATUS OF *ORNITHORHYNCHUS AGILIS* DE VIS, 1885 AND SELECTION OF A LECTOTYPE

De Vis (1885: 35-8) describes a right tibia (F706) and a right dentary fragment (F707) from Pleistocene deposits at Kings Creek, Pilton, on the Darling Downs, Queensland (Plates 3-4). Comparison with a larger Queensland Museum sample of *Ornithorhynchus anatinus* than was available to De Vis suggests *agilis* should be placed in the synonymy of *anatinus*. The fossil tibia (F706) can be matched in virtually every respect with (for example) the tibia of J2414. All of the muscle scars are closely comparable. The only noticeable difference is the slightly smaller size of the fossil tibia.

The fossil dentary fragment (F707) shows, according to De Vis (1885), evidence of four sets of alveoli rather than the three of the modern platypus. The evidence for this is the very slightly raised ridges between the alveolar depressions. However, from a sample of six modern platypuses it is clear that these ridges are variable in the extent of their development and completely unreliable as indicators of tooth number or even constancy of alveolar sets. However, the actual number and disposition of alveolar depressions does seem to be reasonably constant. Clearly the normal condition is for five lingual and four buccal depressions. The shallow posterior lingual depression is the terminal depression of the alveolar area. There is also probably a relationship between the number and disposition of these depressions and the root morphology of the deciduous teeth (e.g. Green 1937), such that the last lingual depression corresponds with the small M_1 ; the preceding two lingual and two buccal depressions correspond with M_2 ; and the anterior two lingual and two buccal depressions correspond with M_3 . The number and disposition of the alveolar depressions in F707 are identical to those of the modern platypus.

De Vis (1885) also regards the angular process of the fossil dentary (F707) to be larger than it is in the modern platypus. The larger modern sample however does not support this assertion, the angular process being as well-developed (merely a raised ridge) in, for example, J16700 as it is in the fossil dentary (F707). Interestingly, as noted above, a larger, better-defined angular process is a diagnostic character of *Obdurodon insignis*.

Dentary fragment F707 is here selected as the lectotype of *Ornithorhynchus agilis* De Vis because of the better representation of dentaries in modern and fossil comparative collections.

With synonymy of *Ornithorhynchus agilis* De Vis in *O. anatinus*, *Obdurodon insignis* Woodburne and Tedford becomes the only known species of fossil ornithorhynchid.

OBDURODON INSIGNIS

ACKNOWLEDGEMENTS

Stephen Van Dyck (Queensland Museum), Richard Brown (Bureau of Mineral Resources), and Alex Kowanko (South Australian Museum) helped in the recovery of the fossil samples from SAM Quarry North. Mr Brian and Ms Kath Oldfield most generously allowed us to work on Etadunna Station. Mr Alan Easton (Queensland Museum) took the photographs. The manuscript was read by Merv. Griffiths (C.S.I.R.O.), Alan Bartholomai (Queensland Museum), Michael O. Woodburne (University of California at Riverside), and Richard H. Tedford (American Museum of Natural History).

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PLATE 1

A, D and H, stereophotos of F9558, the left dentary fragment referred to *Obdurodon insignis*, preserving the alveoli for M_3 , M_2 and the posterobuccal alveolus for M_1 . B and E, stereophotos of J23753, a left dentary of a juvenile *Ornithorhynchus anatinus* showing the alveolar areas for M_{1-3} . C, F and H, stereophotos of a left dentary fragment of J20672, an adult *O. anatinus* with alveoli for M_{2-3} . Abbreviations: *ap*, angular process; *ic*, internal coronoid process; *mc*, mandibular canal; m_1 , the alveolar area for M_1 (four depressions in the modern platypus, one alveolus in F9558); m_2 , the alveolar area for M_2 (four depressions in the modern platypus and four alveoli in the fossil); m_3 , the alveolar area for M_3 (one depression in the modern platypus, one alveolus in the fossil). Twice natural size.

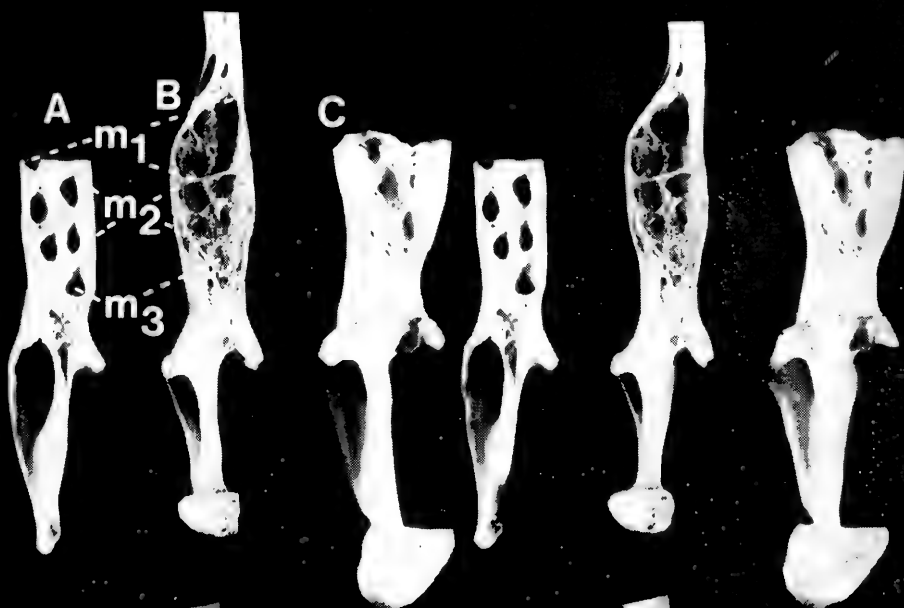


PLATE 2

A and B, postero-oblique stereophotos of (A) F9558, and the left dentary fragment of *Obdurodon insignis*, and (B) J20672, the left dentary fragment of *Ornithorhynchus anatinus*, to show the difference in size of the mandibular foramen and angular process. C and D, stereophotos of the medial face of (C) F9559, a left ilium referred to *Obdurodon insignis*, and (D) J811, the left ilium of a juvenile *Ornithorhynchus anatinus*. E and F, stereophotos of the lateral face of (E) F9559, the fossil ilium and (F), the anterior part of the pelvis of an adult *O. anatinus*. Abbreviations: *ac*, anterior part of the acetabulum; *ap*, angular process; *ax*, the sacral axis (see text); *c*, area of a attachment for the centra of the first and second sacral vertebrae; *gf*, gluteal fossa, the area for attachment of, among other muscles, the powerful gluteus medius; *if*, iliac fossa, the area for attachment of the powerful iliacus and psoas muscles; *ih*, distal iliac head, an area for attachment of various muscles (see text) including the ilio-costalis and cruro-coccygeus; *mf*, mandibular foramen; *rf*, scar for the rectus femoris; *sa*, area on the medial face of the ilium between the two points of attachment of the ilium to the sacrum and forming the lateral wall of the sacral arcade; *t*, area of attachment for the transverse process of the first sacral vertebra. Twice natural size.

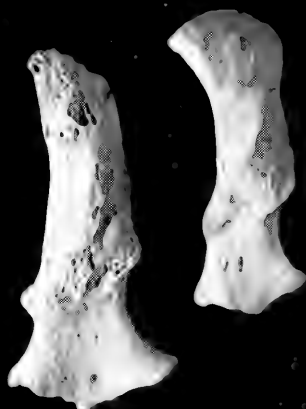
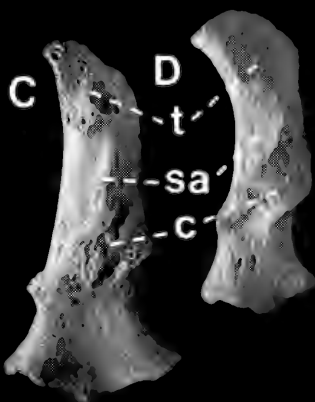
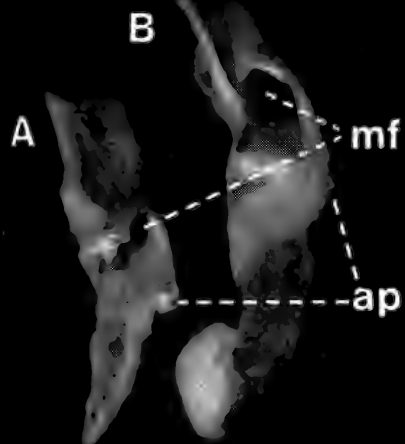
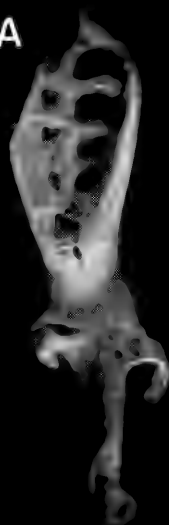


PLATE 3

A and B, stereophotos of F707, the lectotype of *Ornithorhynchus agilis* De Vis, a right dentary fragment preserving the alveolar areas for M_{1-3} showing the (A) occlusal, and (B) occluso-medial views. Twice natural size.

A



B

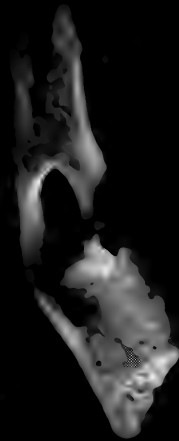
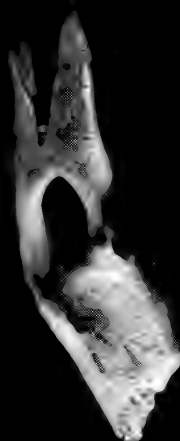
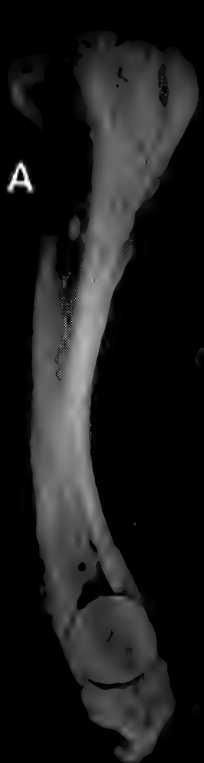


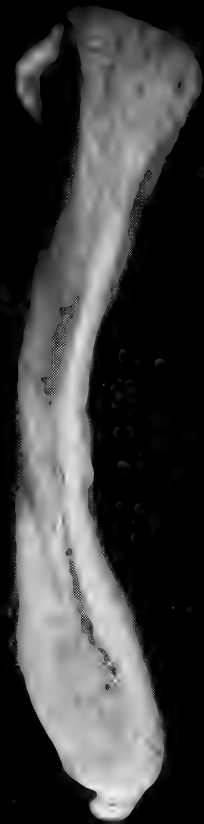
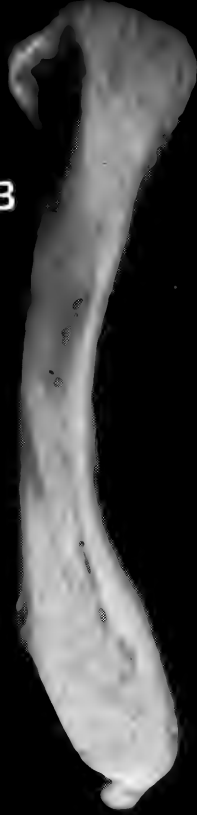
PLATE 4

A and D, stereophotos of F706, the paratype of *Ornithorhynchus agilis* De Vis, a right tibia showing (A) an antero-external view, and (D) a postero-internal view. B and C, stereophotos of J2414, a right tibia of *Ornithorhynchus anatinus*. Twice natural size.

A



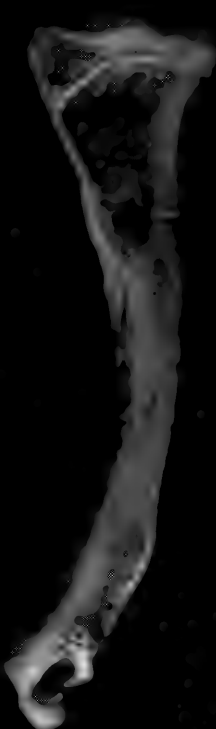
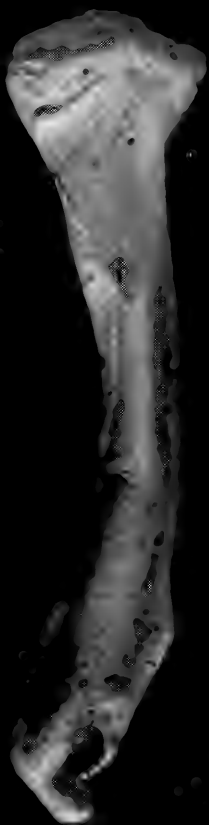
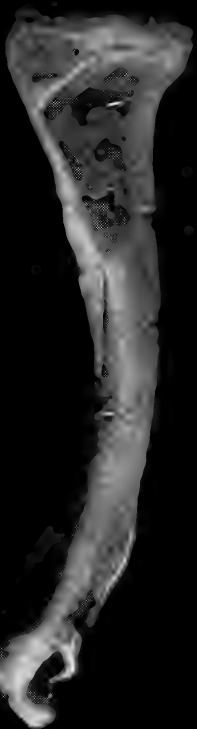
B



C



D



Late Cenozoic Monotreme Anteaters

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ABSTRACT

Five species and possibly three genera of echidnas were present in the late Cenozoic of Australia. *Zaglossus bruijini* makes an appearance in the late Pleistocene of New Guinea and perhaps in some late Pleistocene localities on the Australian continent. *Zaglossus ramsayi* is the most abundant fossil species. It appears to have become extinct in the upper Pleistocene possibly shortly after having given rise to *Zaglossus bruijini*. Closely related and perhaps ancestral to *Zaglossus ramsayi*, *Zaglossus robusta* may be as old as Pliocene. The extremely large species, *Zaglossus hacketti* is sufficiently different from *Zaglossus* and *Tachyglossus* to merit a separate generic distinction. The genus *Tachyglossus* is present in the late Pleistocene, but is nowhere common as a fossil.

A "gigantic" species of fossil echidna was described by Krefft in 1868. This discovery took place in Australia about eight years before a "trophy skull" of a similar species, apparently still living on the island of New Guinea, was described by Peters and Doria in 1876. Since then small collections of *Zaglossus bruijini* skeletal material have accumulated in a few museums and universities around the world.

Krefft's fossil specimen consists of a fragment of the distal portion of a right humerus recovered from Pleistocene fluviatile deposits in Darling Downs, Queensland. The fossil preserves the condyle of the humerus which resembles that of the living species, *Zaglossus bruijini*. The fossil was named *Echidna owenii* after the famous anatomist (Krefft, 1868; Peters and Doria, 1876).

More than eighty fossil specimens of large echidnas have been accessioned in museum registers since that time. Additional, often fragmentary and unrecognised material from a number of Late Quarternary cave deposits lies unrecorded in bulk collections of vertebrate remains (Table 1).

A large number of species have been attributed to the now invalid genus *Echidna*, which has remained in use for some of the fossils. The fragmentary condition of the type material is the primary reason for the proliferation of synonyms. Also, because there were no associated remains until very recently, each new discovery, whether femur, humerus or cranium was designated a new species. The

TABLE 1

Fossil echidna remains in Australian museums.

NATIONAL MUSEUM OF VICTORIA		
Element	Locality	Registration No.
Humeri (5L, 4R)	Strathdownie Fissure, Vic.	20 555-9/20 564-6
Ulnae (4L, 1R)	" " "	20 567-20 570/20 592
Crania (3)	" " "	20 560-2
Radii (2R, 1L)	" " "	20 571-2/20 593
Scapulae (4L, 1R)	" " "	20 573-6/20 577
Femur (1L)	" " "	20 578
Tibiae (2L, 6R)	" " "	20 579-20 580/20 581-6
Fibulae (3R)	" " "	20 587-9
Atlas (1)	" " "	20 590
Epiporacoid (1)	" " "	20 591
AUSTRALIAN MUSEUM		
Femora (2R)	Wellington Caves, N.S.W.	F.13580/F.10888
Humerus (1R)	Darling Downs, QLD.	F.11017
Humerus (1L)	Wellington Caves, N.S.W.	F.10948
Humerus (1R)	Canadian Deep Lead Mine, N.S.W.	F.51453
Atlas (1)	" " " "	F.51452
Cranium (1)	" " " "	F.51451
SOUTH AUSTRALIAN MUSEUM		
Cranium (1)	Fox Cave, South Australia	P19024
Humeri (2), Ulnae (2)	" " " "	P19021
Tibia (1), Ulnae (2)	Henschke's Quarry Cave, S.A.	P17650
Femur (1), Ulna (1)	" " " "	P18576
Humerus (1R)	" " " "	P18579
Humerus (1)	" " " "	P18602
Ulna (1)	" " " "	P19307
TASMANIAN MUSEUM		
Partial associated skeleton, 14 elements including cranium, humeri, femora, tibiae, etc.	Montagu Caves, N.W. Tas.	Z.2031
Cranium (1)	" "	Z.2032
Humerus (1)	" "	"
Scapula (1)	" "	"
QUEEN VICTORIA MUSEUM		
Femur (1)	Scotchtown Cave, N.W. Tas.	_____
Femur (1)	Egg Lagoon, King Island	1965:39:5
WEST AUSTRALIAN MUSEUM		
Atlas (1)	Mammoth Cave, West Australia	60.10.1
Clavicles & episternum		
Innominate (1)		
Femora (2)		
Tibia (1)		
Radius (1)		

FOSSIL ECHIDNAS

recovery of new material was helped to clarify taxonomic relationship of some of the fossils, but many problems still remain.

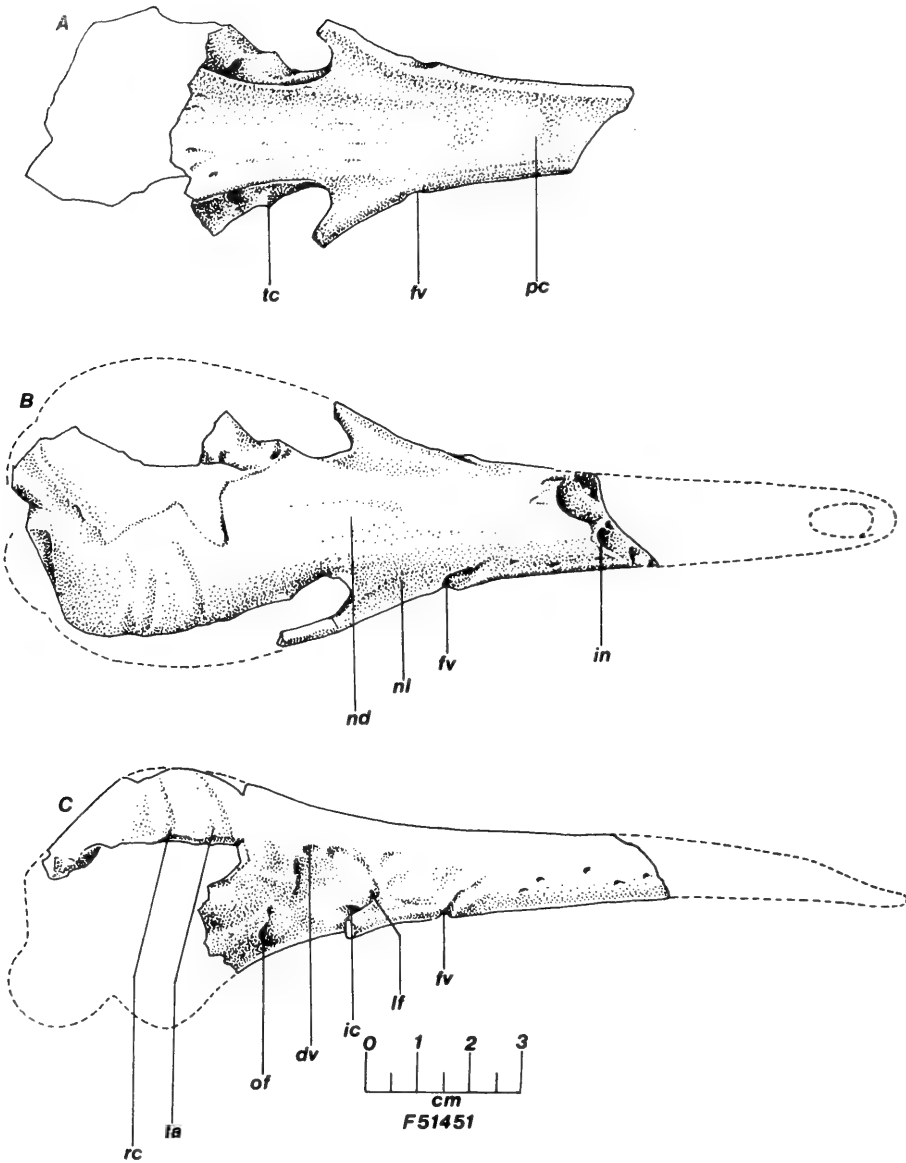
Reassessment of the fossil material is made difficult not only by its fragmentary condition but especially by the lack of stratigraphic control. I have presented a brief description of both "old" and "new" specimens upon which the tentative systematic revision given here is based. At present, there is not enough complete material to permit statistical verification of the populations here defined. I have also attempted to restore certain attributes of the fossil species' appearance and feeding mechanism. A final, equally speculative section of this paper examines some possible causes of extinction of the genus on the Australian mainland.

In the text, and in some illustrations I have referred to individual specimens by their original names to avoid confusion. The genus *Zaglossus* has already been confounded by having at least three synonyms simultaneously in use before the turn of the century.

FOSSIL ZAGLOSSUS CRANIA

The holotype of *Echidna* (*Proechidna*) *robusta* Dun 1895, (cranial fragment, A.M. No. F.51451) from the Canadian Deep Lead Mine Shaft, Gulgong, N.S.W. (Fig. 1) was the only fossil tachyglossid cranium known until recently. This imperfect cranium has been reconstructed using information from recently recovered cranial material (Fig. 2). A brief redescription of the fragment may therefore be of interest. F.51451 differs from *Zaglossus bruijini* in having a broader rostrum with a more abrupt taper to the sides. If lines drawn parallel to the margins of the beak are continued until they intersect, the resulting triangle is relatively short in proportion to the breadth of its base, being more like *Tachyglossus* than *Zaglossus bruijini* in this respect (Fig. 3). In transverse section, the outline of the deeply arched palatal roof is parabolic. A similarly positioned section through *Zaglossus bruijini* is shallower and shaped like an inverted "V" or "gabled". The posterior portion of the palate of *Echidna robusta* is curved as in *Zaglossus bruijini*. However, the anterior portion of the palate appears to be perfectly straight in contrast to *Z. bruijini* in which this portion of the palate shows a continuation of the arc commencing further back. This uniform decurvation extends to the tip of the snout in *Z. bruijini*, whereas in *E. robusta*, as inferred from a closely related complete specimen (T.M. No. Z.2031, Fig. 2), slight curvature may have been present in the distal third of the rostrum (Figs. 1C, 4A, 5A), (Murray, 1978).

The length of the rostrum of the Gulgong fragment has been restored by projecting the straight sides of the rostrum of Z.2031. The percentage of the length of the resulting triangle occupied by the rostrum of this complete specimen was used to calculate the length of the missing portion of F.51451 (Fig. 3). An estimated condylobasal length of 200.0 mm. was obtained from *E. robusta*. This is at least 3.0 mm. shorter than the longest complete *Z. bruijini* skull in the AMNH collection and perhaps well below the two specimens mentioned by Van Deussen



and George (1969) that would have exceeded 230.0 mm. in length had they been perfect.

The Montagu, Tasmania, specimen (T.M. No. Z.2031) has recently been described in detail (Murray, 1978), (Figs. 2, 4c, 5b). The skull is smaller (165.0 mm. condylobasal length, Table 2) but otherwise very similar to F.51451. The known size range of *Zaglossus bruijni* skulls would exceed the differences in length between Z.2031 and F.51451 (Fig. 5). However, there are some proportional differences between the width of the palate and rostrum. The height of the braincase is proportionally low compared to Z.2031. This is probably a size-related feature as is the broader, deeper fossa for the nasolabialis muscle.

In general, Z.2031 differs from *Z. bruijni* in precisely the same characteristics as described for F.51451: the rostrum of Z.2031 is broad, relatively short and only slightly decurved; the occipital condyles are long and narrow and the palate is broad and deeply arched rather than narrow, shallow and gables shaped in cross-section (Fig. 4).

FIG. 1.—Drawing of a late Cenozoic fossil tachyglossid, *Echidna* (*Proechidna*) *robusta* = *Zaglossus robusta* Dun Australian Museum F.51451); A. palatal aspect; B. dorsal aspect; C. lateral aspect.

Abbreviations:

adm	great diploic artery
af	anterior palatine fenestra
at	tympnic aperture of the facial canal
cp	crista parotica
ct	temporal canal
dg	dorsomedian groove
dv	diploic vein foramen
ep	ectopterygoid
fo	foramen ovale
fs	sphenopalatine foramen
fsp	primitive stylomastoid foramen
fv	facial vein groove
ic	infraorbital canal
in	internal nares
jf	jugular foramen and fenestra
lf	lacrimal foramen
mf	maxillofacial foramen
na	external nares
nd	nasofrontal depression
nf	nasofrontal foramina
nl	"nasolabial" fossa
of	optic fissure
on	orbitonasal foramen
pc	palatine corrugation
pt	pterygoid canal
rc	rectus cervicis crest
re	epitympanic recess
ta	trapezius anterior crest
tc	temporalis crest
tf	tympnic fossa
vf	vestibular foramen

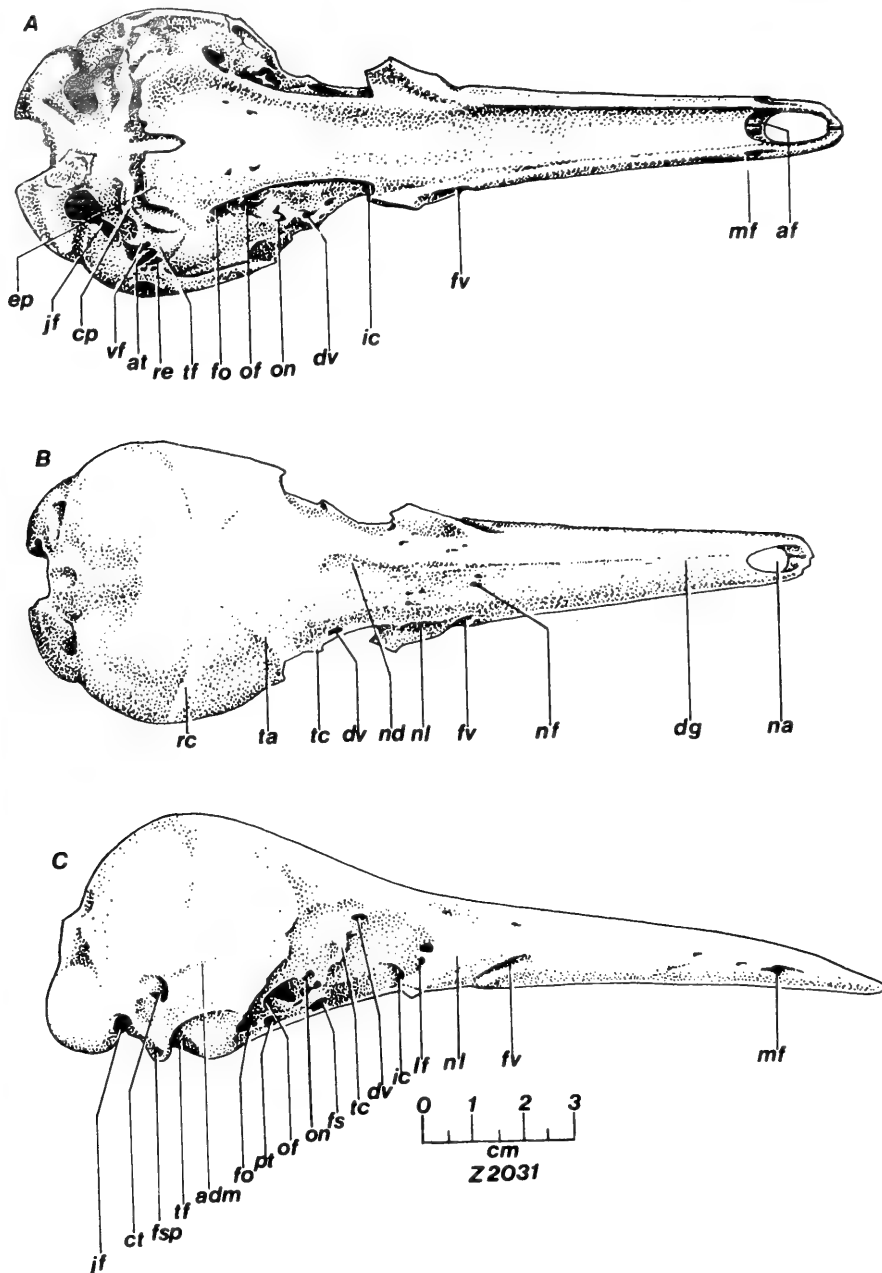


FIG. 2.—Drawing of a late Pleistocene fossil tachyglossid, *Zaglossus ramseyi* (Tas. Mus. Z.2031); A. palatal aspect; B. dorsal aspect; C. lateral aspect. Abbreviations as given for Fig. 1.

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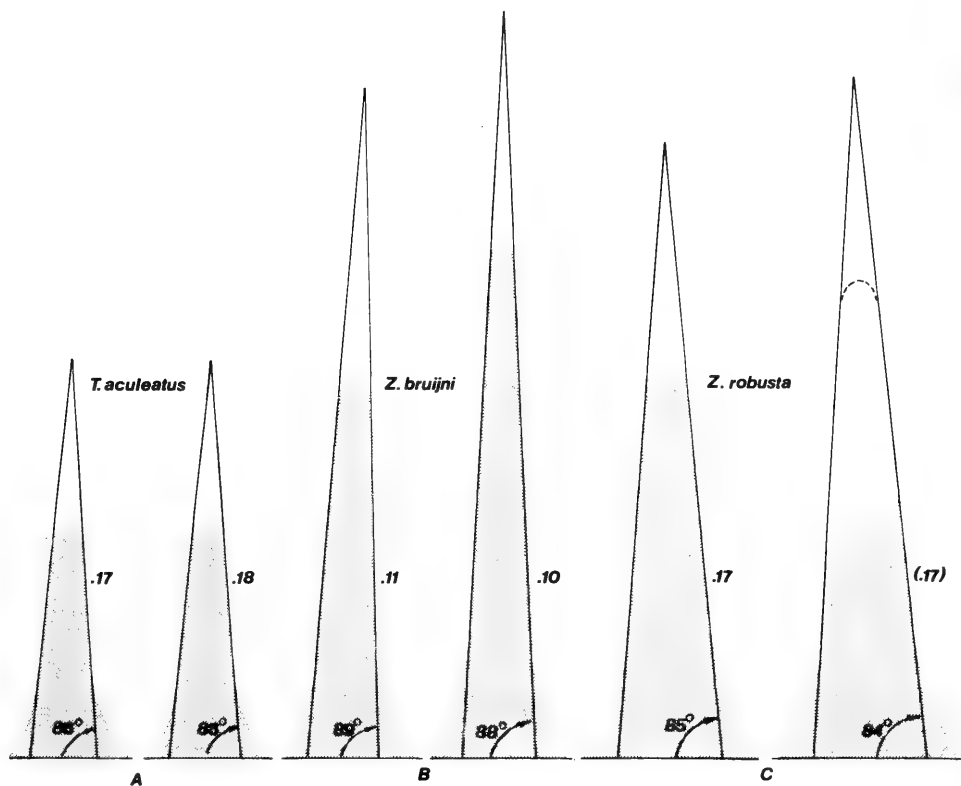
TABLE 2

CRANIAL MEASUREMENTS OF FOSSIL *ZAGLOSSUS* SPECIMENS

	F.51451	Z.20.31	P19024
Width rostrum	25.5	21.5	16.9
Width palate	24.5	23.2	14.5
Thickness maxillary process	5.5	3.5	—
Depth palatal arch	7.1	4.7	3.0
Height rostrum 1	16.2	14.1	—
Height rostrum 2	21.0	20.2	—

Height rostrum 1 = height at facial vein groove;

Height rostrum 2 = height at level of infraorbital canal.

FIG. 3.—Comparison of the proportions of the rostrum and method of estimating the length of the rostrum of F.51451; A-B. *Tachyglossus*; C-D *Zaglossus bruijini*; E. *Zaglossus ramsayi*; F. *Zaglossus robusta*.

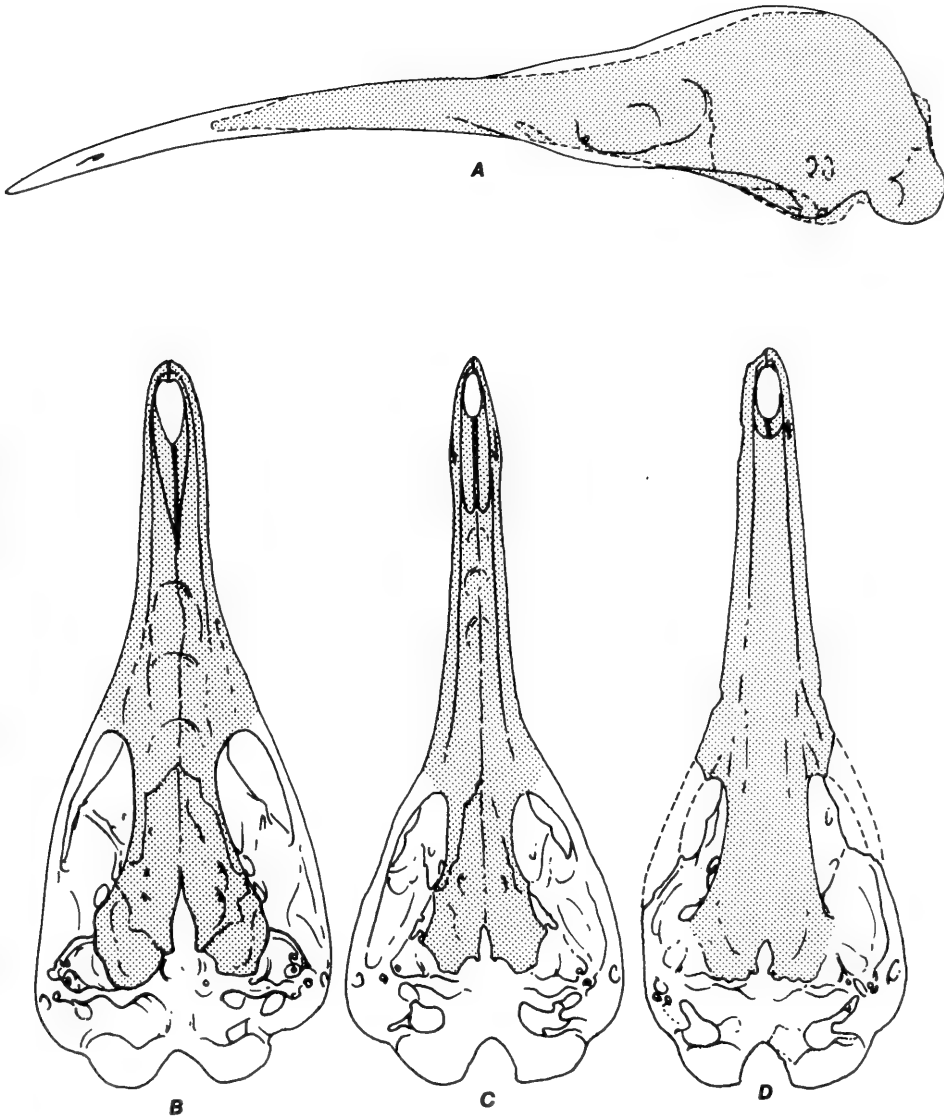


FIG. 4.—A. comparison of *Zaglossus ramsayi* and *Zaglossus bruijni* proportions; interrupted outline with tone represents Z.2031, *Zaglossus bruijni* after natural-sized lithograph in Gervais, 1878; B. comparison of proportions of neurocranium to visceral cranium in a. *Tachyglossus*; b. *Zaglossus bruijni* (Aust. Mus. M.9852); c. *Zaglossus ramsayi*, scales adjusted to equal condylobasal lengths.

FOSSIL ECHIDNAS

Cranial fragments of apparently smaller or more gracile individuals have been recovered from Late Pleistocene localities in South Australia and Victoria. A maxillary fragment from Strathdownie fissure (one of a series N.M.V. No(s) 20560-62) figured in a National Museum of Victoria information pamphlet, closely resembles *Zaglossus bruijni*. Unfortunately, the specimen can no longer be located (T. Rich, personal communication).

A specimen having apparently similar proportions from Fox Cave, South Australia (S.A.M. No. P19024) is within size range of *Zaglossus bruijni*. In cross-section, the base of the rostrum appears to be shallower than a similar section through Z.2031, and it is somewhat gable-shaped rather than smoothly arched. Unfortunately, the rostrum is broken just anterior to the root of the zygoma, and the palatal section characteristic is less reliable here than just a few centimeters distally.

The small amount of cranial material available consists of three forms that appear to have a degree of morphological and metric overlap. Further evidence for the existence of these populations is present in the postcranial remains.

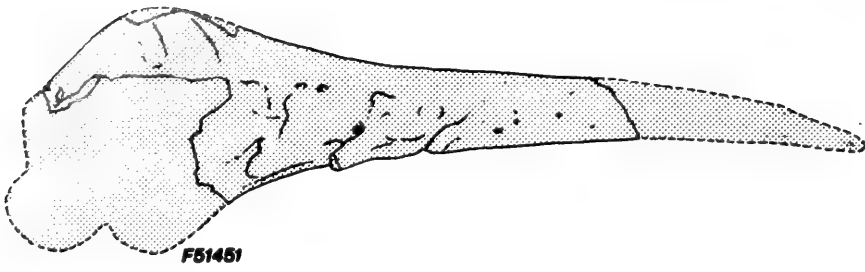
ZAGLOSSUS POSTCRANIAL REMAINS

The holotype *E. (Proechidna) robusta* humerus was originally described as a giant platypus (Dun, 1895). Gill and Mahoney recognised that *Ornithorhynchus maximus* was clearly a tachyglossid and that it "... possibly belongs to the same individual as the type material" (Mahoney and Ride, 1975). The humerus corresponds with the cranium in extent and type of permineralisation, colour and large size. Except for its large size and a relatively enlarged posterior opening of the entepicondylar foreamen, there is no other characteristics that would differentiate

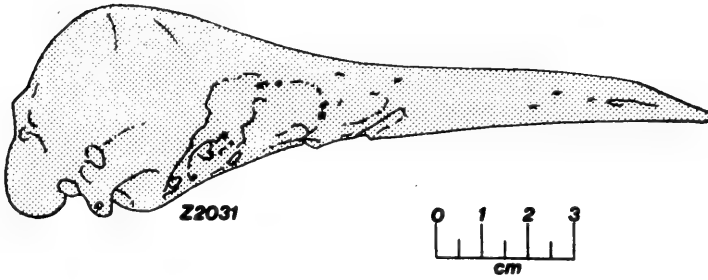
TABLE 3

	F.51453	Z.2031	P18579	P18602	F.10948
Dimensions head	28.5/19.0	26.2/15.1	23.8/13.0	—	26.7/13.3
Lesser tub. — head	15.0	14.4	—	—	—
Lesser tub. — t.m.	31.5	28.1	—	—	—
Width diaphysis	23.0	20.7	18.1	—	—
Height entepicondyle	21.0	26.0	23.9	—	24.0*
Height ectepicondyle	18.4	19.6	—	—	—
Length condy. — head	72.0	66.5	62.5	—	70.0*
Length flexor tubl. — head	79.5	77.0	70.5	—	83.0
Dimensions ent. for. (post.)	06.0/7.0	03.4/3.4	—	—	03.0/3.7*
Dimensions ent. for. (ant.)	07.8/7.0	04.9/4.6	—	—	06.0/6.0
Width across epicondyles	70.5*	—	—	68.5*	—
Width across tuberosities	48.6	—	—	—	—

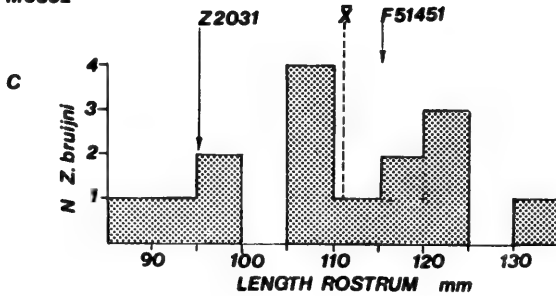
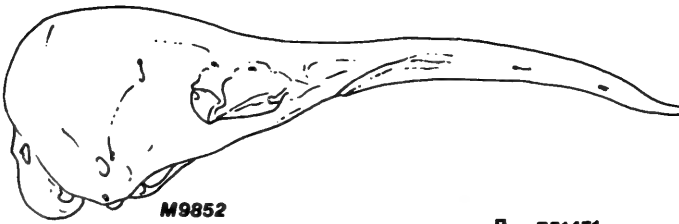
Abbreviations: tub., tuberosity; t.m., teres major tubercle; condy., condyle; tubl., tubercle; ent., entepicondylar; post., posterior; ant., anterior; for., foramen.



A



B



it from the humerus of *Tachyglossus*. An additional peculiarity of the fossil, the slenderness of the entepicondyle (Fig. 6) is often duplicated in the humeri of the latter species. In any case, the morphology of the entepicondyle and its foramen does not closely resemble that of *Ornithorhynchus* (Fig. 6 E, F).

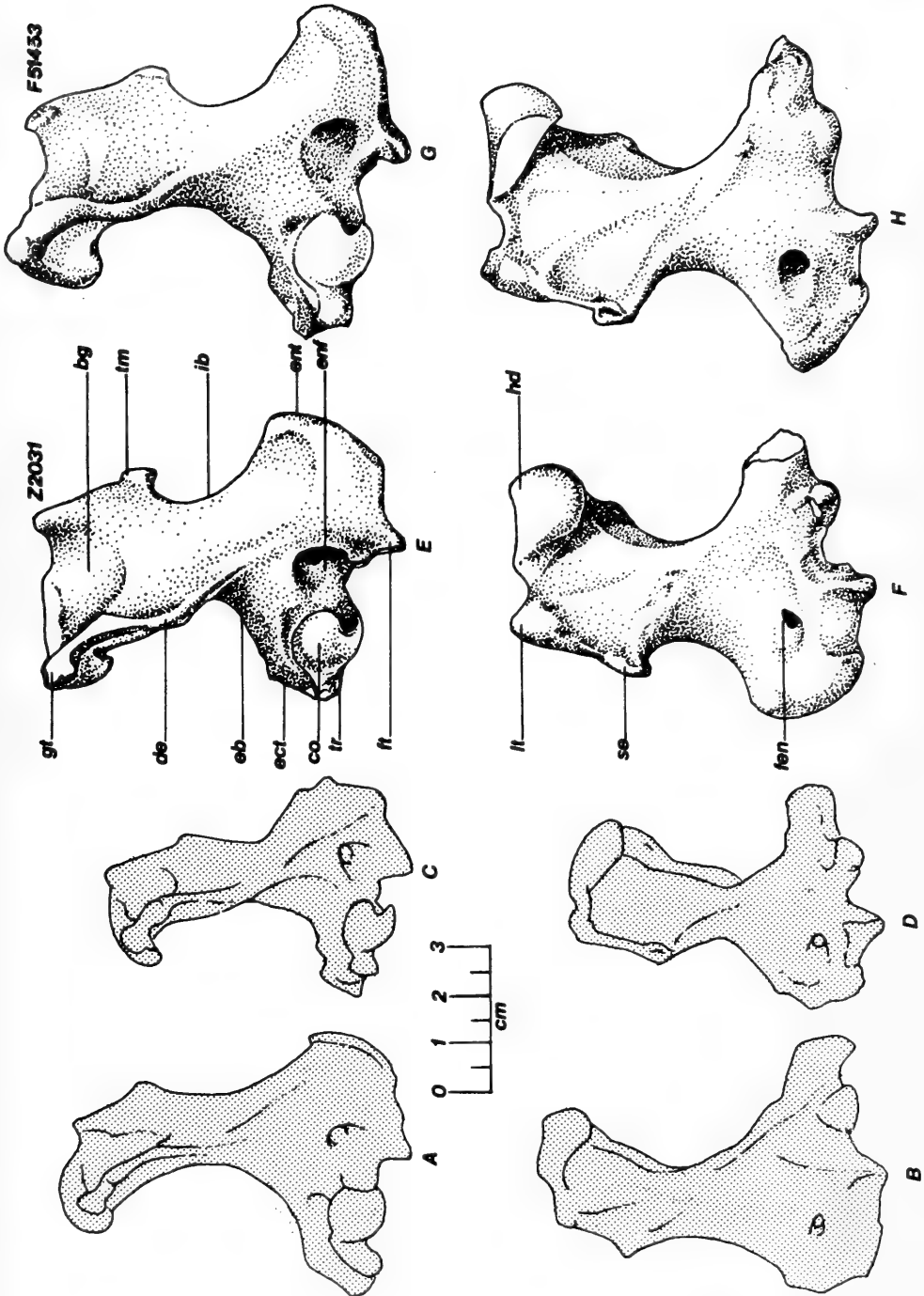
The shape and proportions of the entepicondyle of the tachyglossid humerus appears to be extremely variable. Dun (1895:124) was apparently aware of this in stating that the "... form of this bone varies very much in these genera."

The holotype of *Echidna ramsayi* (A.M. No. F.10948) is very similar to *Ornithorhynchus maximus* in size and morphology (Table 3). Damage to the upper portion of the entepicondyle does not allow comparison with F.51451. The entepicondylar foramen is very small in diameter on the posterior side but quite the same in size and shape on the anterior side.

Dun (1895) placed *E. ramsayi* in *E. owenii* (A.M. No. F.11017). However, it is probable that the specimen is too fragmentary to permit distinctions to be made at the species level. The humeral condyle, which is all that is taxonomically significant about the fossil (except for size) is very similar to that of *E. ramsayi*, *E. robusta* and *Z. bruijini*. The specimen appears to differ from *E. robusta* in having a narrower, deeper concavity between the condyle and the beginning of the entepicondyle. The condyle of *E. robusta* also appears to be slightly narrower. However, these characteristics may merely represent individual variation. While it looks as though *E. owenii* and *E. ramsayi* represent the same species, the fact that this cannot be formally demonstrated at this time is sufficient reason to not lump them. This stand is bolstered by the problematic presence of two very similar morphs of the genus in the late Pleistocene.

The humeri associated with the cranium from Montagu Caves, Tasmania (T.M. No. Z.2031) clearly belong to the same species as F.10948, *Echidna ramsayi* (Figs. 6, 10). The Montagu humeri are slightly smaller (Table 3) but otherwise morphologically identical. The entepicondylar foramen of Z.2031 appears to be absolutely larger than that of F.10948, but smaller than that of *Ornithorhynchus maximus*. The entepicondyle of Z.2031 is wider than that of F.51453 (Fig. 6E-G) but this range of variation does not appear to greatly exceed that of *Zaglossus bruijini* (Fig. 6A-D).

FIG. 5.—Comparison of the range of variation in crania of the living species, *Zaglossus bruijini* with the differences between two fossil species, *Zaglossus robusta* and *Zaglossus ramsayi*. Note that the fossil specimens lie well within the range of lengths obtained from *Z. bruijini* crania; A., a lateral view of *Zaglossus robusta* (restored) and b. *Zaglossus ramsayi* compared with B. lateral views of a. *Zaglossus bruijini* (after Gervais, 1878); b. *Zaglossus bruijini* (Aust. Mus. M.9852); C. histogram depicting range of variation of length in *Zaglossus bruijini*, arrows indicate lengths of fossil crania (Z.2031 = *Zaglossus ramsayi*; F.51451 = *Zaglossus robusta*).



A proximal fragment of left humerus from Henschke's Quarry Cave, Nara-coorte S.A., (S.A.M. No. P18602) though broken across both epicondyles is still nearly as broad as the almost complete *O. maximus* humerus. Undamaged, this specimen would have been similar in size and proportions.

Again it is not possible to compare the upper borders of the entepicondyle due to extensive damage to that portion of the specimen. While very large, the fragment may not represent either *E. ramsayi* or *E. robusta*. The specimen is a good match for size with that of a very large "gracile" femur from the same deposit.

The humeri of *E. ramsayi* and *E. robusta* can be distinguished from those of *Z. bruijni* by their broader diaphyses, deep, 'comma-shaped' internal border and more prominent crests formed by the greater and lesser tuberosities (Fig. 6). Whereas a *Z. bruijni* humerus may equal or exceed the length of *E. ramsayi* or *E. robusta*, none would have as great a breadth of the shaft or processes for muscular attachment so robust and prominent.

A nearly complete humerus from Henschke's Quarry Cave (S.A.M. No. P18579) is intermediate between *E. ramsayi* and *Z. bruijni* with respect to robusticity ($W/L = 0.26$, compared with 0.20 for *Zaglossus bruijni* and 0.29 for Z.2031 and F.51453). Thus, while the specimen is about the same size as *Zaglossus bruijni*, it gives the impression of being more compact or stout than the humeri of that species. I suggest that it is the humerus of an immature *E. ramsayi* or that of a small individual rather than a representative of a population in transition to *Z. bruijni*. However, its height in the stratigraphy of the cave (0-20" makes the latter interpretation for the fossil very attractive.

FIG. 6.—Comparison of right humeri of living and extinct species of *Zaglossus*, anterior surface above, posterior surface below; A-B. *Zaglossus bruijni*; C-D. *Zaglossus bruijni*; E-F. *Zaglossus robusta* (F.51451); G-H. *Zaglossus ramsayi* (Z.2031).
Abbreviations:

bg	bicipital groove
co	condyle
de	deltoid crest
eb	external border
ect	ectepicondyle
enf	entepicondylar fossa
ent	entepicondyle
fen	entepicondylar foramen
ft	flexor tubercle
gt	greater tuberosity
hd	head
ib	internal border
lt	lesser tuberosity
se	sesamoid
tm	teres major tubercle
tr	trochlea

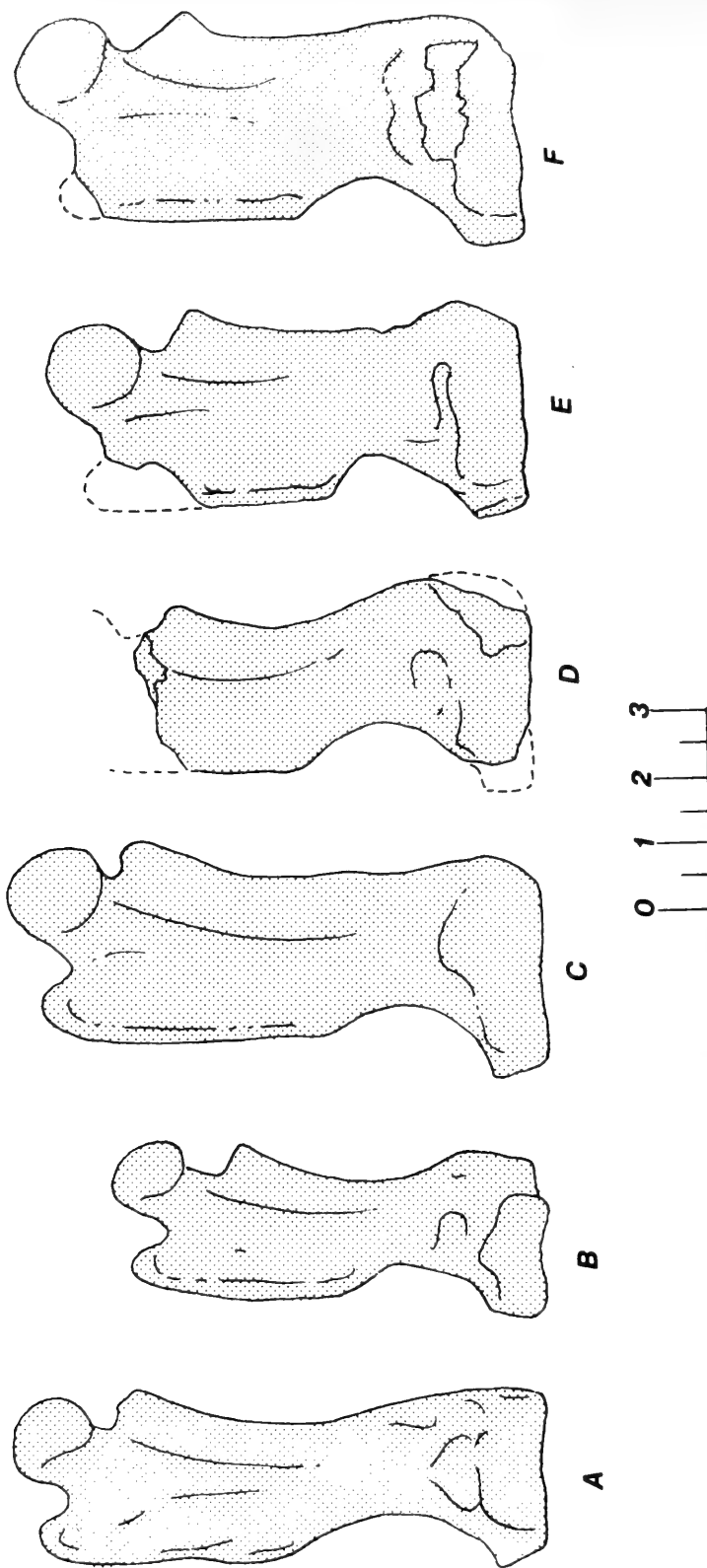


FIG. 7.—Outline drawings contrasting the size and overall shape of the femora of different *Zaglossus* species; A. *Zaglossus bruijini* (after Gervais, 1878); B. *Zaglossus bruijini* (Aust. Mus. M.9852); C. *Zaglossus* sp. (South Aust. Mus. P19015); D. *Zaglossus ramsayi* (Scotchtown Cave, Tas., Q. Vic. Mus. unregistered); E. *Zaglossus ramsayi* (ex-Z. harrissoni, Q. Vic. Mus. 1965:39:5); F. *Zaglossus ramsayi* (Tas. Mus. Z.2031).

FOSSIL ECHIDNAS

Several unassociated femora have been given species designations. *Zaglossus harrissoni* (Scott and Lord, 1921; Q.V.M. No. 1965:39:5) is the only holotype based entirely on this element. Other assigned femora include *Zaglossus backetti* (Glauert, 1914; W.A.M. No. 60:10:1) and *Echidna ramsayi* (A.M. No. F.13580) which was previously described as *Echidna oweni* by Dun (1895) or as *Zaglossus (Echidna) oweni* by Glauert (1914).

The *Echidna ramsayi* femur is a right proximal fragment missing the greater trochanter and much of the articular surface of the head. The specimen is similar in texture, colour and type and extent of permineralisation to the holotype (F.10948). The diaphysis is broad and the gluteal crest appears to be well developed. *Zaglossus harrissoni* and the associated Montagu femora (Z.2031) have comparably broad, short diaphyses and as far as they can be compared with *E. ramsayi* fragment, they are practically indistinguishable.

TABLE 4
METRIC ATTRIBUTES OF SOME *ZAGLOSSUS* FOSSIL FEMORA

					Scotchtown			
	60.10.1	Nombe	P19015	Z.2031	1965.39.5	Cave	F.10888	P18576
Length (max.)	129.0	83.9	79.0	77.0	70.5	—	—	—
Length gt-c	127.5	—	72.0	71.0	—	—	—	66.0
Width diaphysis	30.5	—	19.8	24.5	22.0	20.5	17.9	23.2
Width condyles	50.5	33.1	34.3	35.8	35.4	—	—	33.7
Width across troch.	48.5	—	34.8	31.5	—	—	28.8	—

Abbreviations: gt-c, greater trochanter to condyles;
Max., maximum; troch., trochanters.

These femora can be distinguished from those of *Zaglossus bruijni* by their much greater ratio of breadth to total length, relatively larger head with a broader neck and deeply sculptured dorsal surface for the attachment of the vastus muscles (Fig. 7, Tables 4, 5). This increased breadth greatly alters the overall appearance of the femur by accentuating the sigmoid shape of the bone.

Small individuals having intermediate attributes and large "gracile" specimens add complexity to the systematics of this group. A right femur shaft from Wellington Caves (A.M. No. F.10888) missing both the proximal and distal articular surfaces is probably an immature specimen of *E. ramsayi*. However, a "gracile" specimen from Nombe Rock Shelter, New Guinea, considerably exceeds in length any of the previously described specimens. This fossil is probably from the late pleistocene (J. Hope, personal communication). A very similar specimen is a right femur from Henschke's Quarry Cave, South Australia, (S.A.M. No. P19015). Both specimens strongly suggest the presence of *Zaglossus bruijni* in the late Pleistocene of Australia and New Guinea. Because of their large size, these specimens

TABLE 5

MORPHOLOGICAL COMPARISON OF LIVING AND FOSSIL TACHYGLOSSID SPECIES

	<i>Zaglossus robusta</i>	<i>Zaglossus ramsayi</i>	<i>Zaglossus bruijini</i>	<i>Tachyglossus aculeatus</i>	<i>Zaglossus hacketti</i>
BEAK	straight, broad, margin angle 84° W/L= est. 0.17	slight decurvation, broad, blunt margin angle 85° ; W/L=0.17	moderate to marked decurvation, pointed margin angle $88-89^\circ$ W/L=0.10-0.11	straight to slightly recurved, very broad, short, blunt at tip; margin angle 86° W/L=0.17-0.18	
PALATE	deep, broad, arched, thick margins	deep, broad, arched thick margins, palatines extend to posterior margin of epipterygoids	moderately deep, gabled section with midline; lateral margins thin; palatines terminate short of posterior margin of epipterygoids	moderately deep, very broad, arched, thick lateral margins, palatines terminate short of posterior margin of epipterygoids	
EAR REGION		tympanic cavity small, very shallow; no overhang of cavity by epipterygoids	tympanic cavity small, shallow; moderate overhang of tympanic cavity by epipterygoids	tympanic cavity relatively large; extensive overhang of cavity by epipterygoid	
HUMERUS	large size, compact; broad diaphysis, W/L=0.29; narrow, tapering entepicondyle, large enteripcondylar foramen; deep, comma-shaped internal border; robust, widely flaring tuberosities	medium to large, compact; broad diaphysis, W/L= 0.26-0.29, wide, squarish entepicondyle, small entepicondylar foramen; deep, comma-shaped internal border, robust, widely flaring tuberosities	medium to large; narrow diaphysis, W/L=0.20; entepicondyle wide, irregularly rounded; small entepicondylar foramen, shallower C-shaped internal border, weaker tuberosities	small size, narrow diaphysis, W/L= 0.19; narrow, tapering entepicondyle, entepicondylar foramen small; deep comma-shaped internal border, robust, widely flaring tuberosities	
FEMUR		medium to large; large head, broad diaphysis, W/L= 0.31-0.32; definite S-shape, trochanters broad, low, equidistant from head; condyles horizontal	medium to large; slender; medium-sized head, narrow diaphysis, W/L=0.20; trochanters equidistant from head; condyles horizontal	small size; slender, narrow diaphysis, W/L=0.17; head large, prominent trochanters equidistant from head condyles horizontal	very large size; head large, low; diaphysis moderately broad, W/L= 0.24; lesser trochanter very low relative to head, lies directly below internal margin; greater trochanter large, high relative to head; flaring medial epicondyle; condyles obliquely oriented
TIBIA		Much longer than femur, FL/TL= 0.78; subround in section DAP/DML=0.94	longer than femur, FL/TL=0.89; subround in section	same length as femur, FL/TL= 1.0; oval in section, DAP/DML= .80	shorter than femur, FL/TL=1.15; flat-tish oval in section, DAP/DML=0.63.

Abbreviations: FL, femur length; TL, tibia length; DAP, anteroposterior dimension; DML, mediolateral dimension; W, L, width and length.

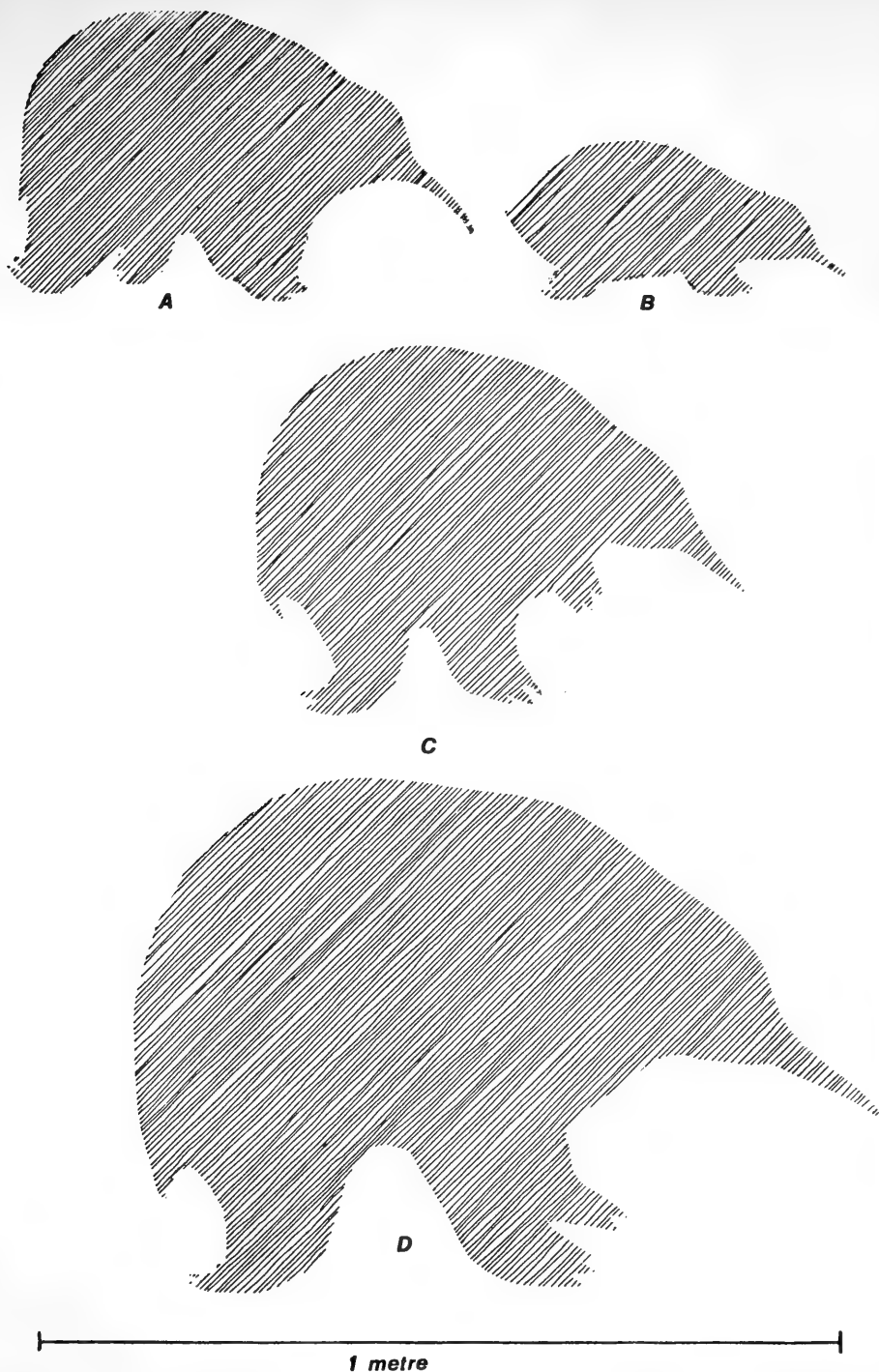


FIG. 8.—Differences in body size of living and fossil tachyglossids: A. *Zaglossus bruijini*; B. *Tachyglossus aculeatus*; C. *Zaglossus robusta* and *Zaglossus ramsayi*, D. *Zaglossus hacketti* (shape of head entirely guesswork).

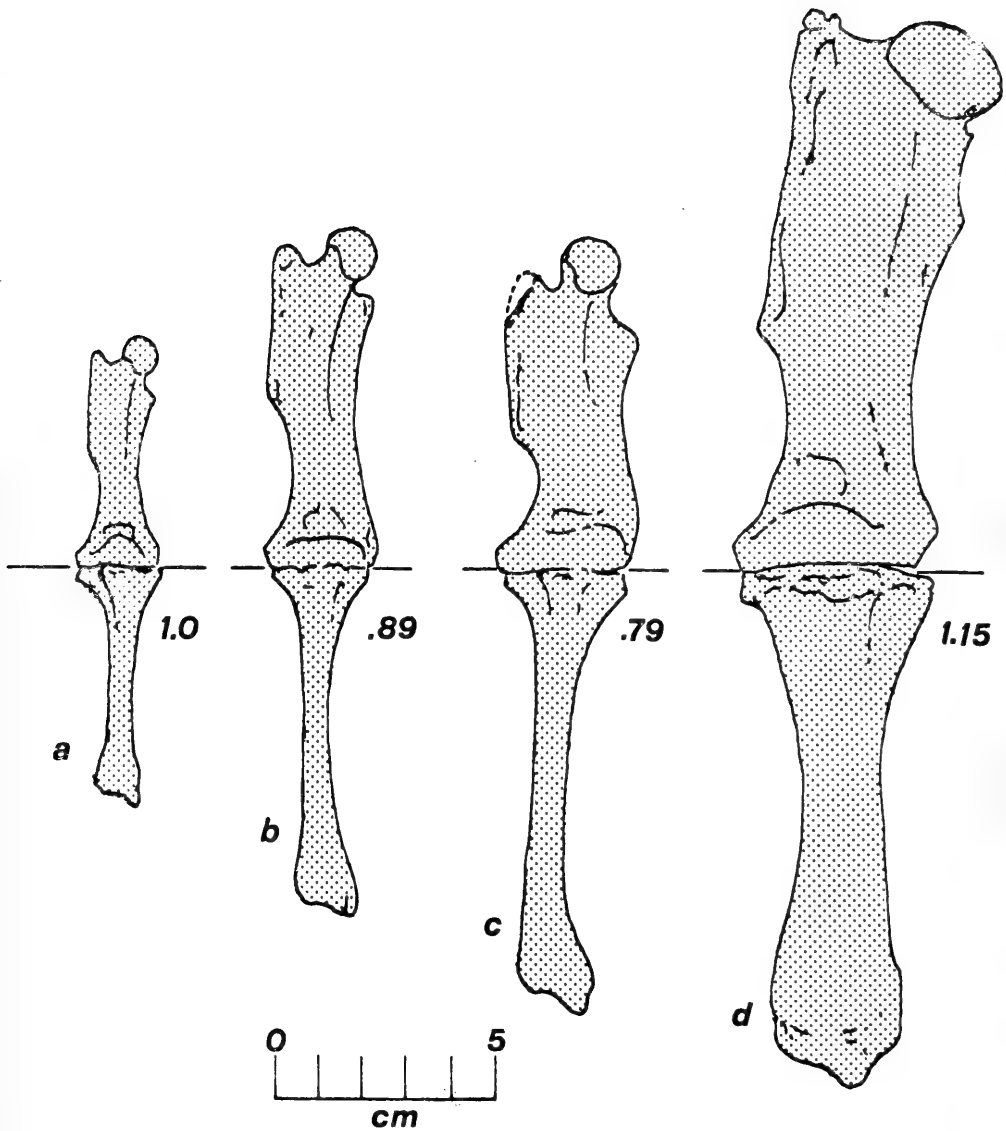


FIG. 9.—Proportions of femur and associated tibia in living and fossil tachyglossids; a. *Tachyglossus*; b. *Zaglossus bruijnii*; c. *Zaglossus ramsayi*; d. "*Zaglossus*" *hacketti*; figures given represent differences in femur and tibia proportions, (FL/TL) obtained by dividing the tibia length into the femur length.

imply that the breadth to length ratio differences observed are not simply size related or allometric features as suggested for F.10888.

The femur of *Zaglossus hacketti* is much larger than that of any other living or extinct tachyglossid known. The large Naracoorte femur (P19015) is only 62% of the length of *Z. hacketti*. By comparison, a femur of a full grown *Tachyglossus aculeatus* is 72% of the length of P19015, thus indicating that the size difference between *Zaglossus* or *Echidna* fossils and *Zaglossus hacketti* was even greater than the difference between *Zaglossus* and *Tachyglossus* (Fig. 8). The femur of *Zaglossus hacketti* is basically tachyglossid in morphology, but differs from both *Tachyglossus* and *Zaglossus* in a variety of features: the medial epicondyle flares outwards and upwards, the lesser trochanter is low and has a weak profile, the head is low and less well differentiated from the shaft and the condyles are obliquely, rather than perpendicularly, oriented relative to the shaft (Fig. 7).

Combined with its associated tibia, the femur suggests that the hind limb proportions differed significantly among these various forms of echidna. In *Tachyglossus* the femur and tibia (Lf/Lt) are equal in length (1.0). in *Z. hacketti* the femur is longer than the tibia (1.15). The associated tibia and femur of Z.2031 (= *E. ramsayi*) yield a very different figure (.79) because the tibia is much longer than the femur in that species. *Zaglossus bruijnii* shows closest affinity with *E. ramsayi* in having longer tibiae than femora (.89), (Fig. 9).

SYSTEMATICS AND EVOLUTION

The geological age of the material ranges from possibly Pliocene (Dun, 1895) to late Pleistocene (Murray, 1978). The Gulgong specimens are believed to be Pliocene on the basis of the estimated age of a basalt flow overlying beds similar to those from which the fossils were recovered. However, some of these flows are also of Pleistocene and even recent age (McAndrew, 1965). Certainly the marsupial fauna from the same locality would not be out of place in Pleistocene deposit (Dun, 1895). In addition there is some fossil material from nearby Wellington Caves that is similar in colour, texture and degree of permineralisation. A re-examination of the entire Canadian deep lead fauna could be of great assistance in concluding this matter. Thus while *E. robusta* could be from Pliocene alluvium, there is considerable room for doubt.

The specimen from Montagu Caves, Tasmania could be as young as 20,000 yr B.P. (Murray and Goede, 1978; Goede, Murray and Harmon, 1978). *Zaglossus hacketti* is probably upper Pleistocene in age (Merrilees, 1968), as is *Zaglossus harrissoni* by analogy with dates obtained from similar N.W. Tasmanian swamp deposits (Gill and Banks, 1956). Most of the material is therefore from the late Quaternary, with the one possible exception being *Echidna* (*Proechidna*) *robusta*.

The foregoing description suggests three morphological categories for the fossil material: (1) a robust form resembling the living species of *Zaglossus* in

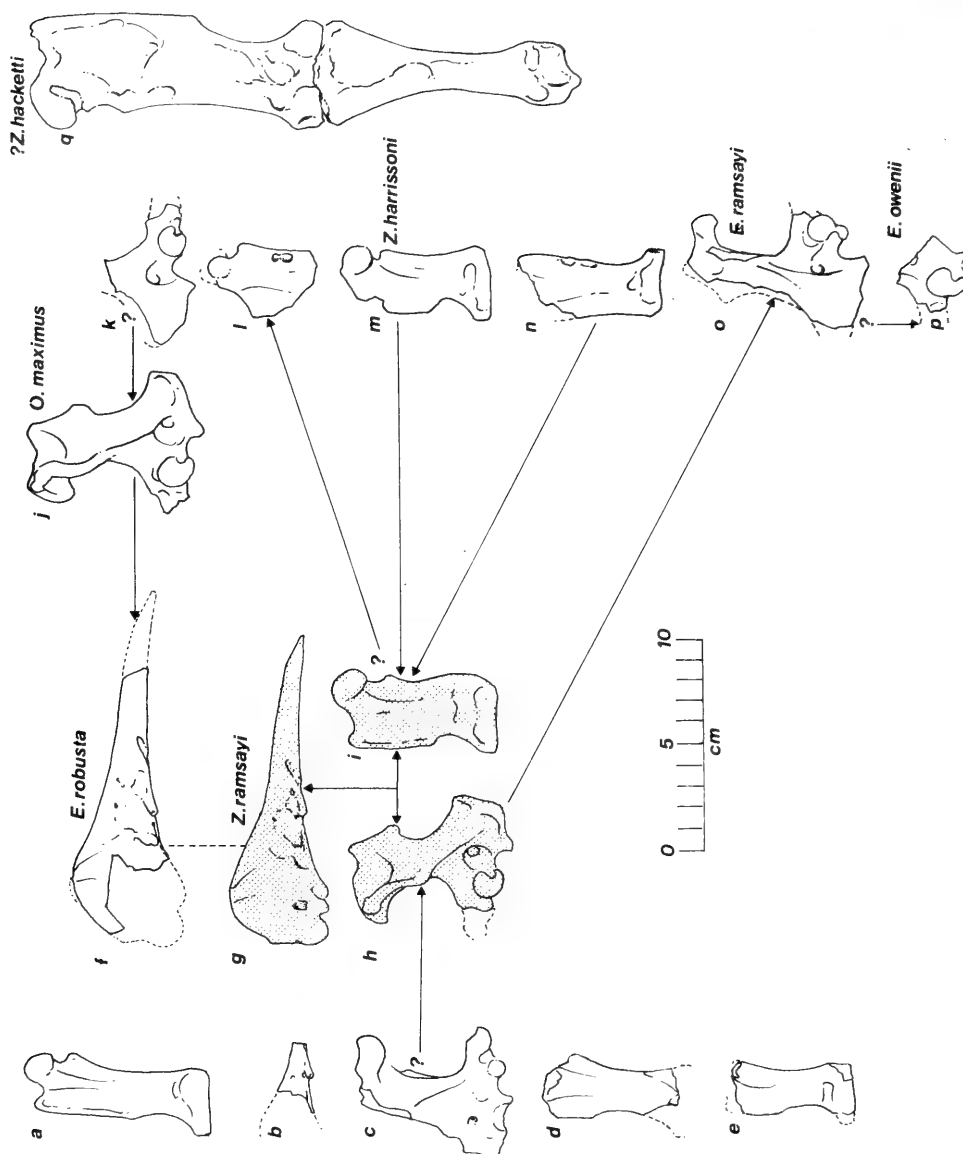


FIG. 10.—Diagram depicting "direction" of comparison of specimens for species assignments; stipple represents associated *Zaglossus ramsayi* remains upon which assignment of isolated postcranial and cranial material is based; a. *Zaglossus* sp. (S.A.M. P19015); b. *Zaglossus* sp. (S.A.M. P19024); c. *Zaglossus* cf. *ramsayi* (S.A.M. P18579); d. *Zaglossus* cf. *ramsayi* (Aust. Mus. F.10888); e. *Zaglossus* cf. *ramsayi* (Scotchtown Cave, Q. Vic. Mus. unregistered); f. *Zaglossus robusta* (Aust. Mus. F.51451); g. *Zaglossus ramsayi* (Tas. Mus. Z.2031); h, i. associated postcranial elements of g; j. *Zaglossus robusta* (Aust. Mus. F.51453); k. *Zaglossus* sp. (S.A.M. P18602); l. *Zaglossus ramsayi* (Aust. Mus. F.13580); m. *Zaglossus ramsayi* (Q. Vic. Mus. 1965:39:5); n. *Zaglossus ramsayi* (S.A.M. P18576); o. *Zaglossus ramsayi* (Aust. Mus. F.10948); p. *Echidna owenii* (Aust. Mus. F.11017, *Nomen vanum*; q. *Zaglossus hacketti* (W. Aust. Mus. 60.10.1).

certain respects but also having some features in common with *Tachyglossus*, such as a relatively broad, blunt beak, little or no rostral decurvation and a deeply arched rather than gable shaped section through the palate; (2) a gracile form of which some specimens are actually larger than those of the robust form, that closely resemble the living species, *Zaglossus bruijni* and (3) a very large species as different from *Zaglossus* as it is from *Tachyglossus* in morphological details and limb proportions.

The generic differences between *Tachyglossus* and *Zaglossus* relate to the morphology of the tongue, body size and shape of the skull (Gill, 1877; Gervais, 1878; Griffiths, pers. comm.). Tongue morphology cannot be directly inferred from the osteological remains. However, the broad, spacious arching palate of *E. robusta* and *E. ramsayi* suggest that the tongue was probably of large diameter or that large food items were being ingested or both. The overall similarity of palatal shape between the fossil echidnas and that of *Tachyglossus* implies a similar feeding mechanism. Many of the apparent differences between *Zaglossus* and *Tachyglossus* are probably due to allometry, analogous to the morphological differences found by Reeve (1940) among small and large genera of South American anteaters. Thus with a moderate increase in body size, the snout may show an impressive increase in length over that of a smaller species with which it is being compared. This kind of proportional relationship between body size and snout length appears to be a partial explanation for the differences in echidna skulls. The robust fossil echidnas appear to be somewhat more likely greatly enlarged *Tachyglossus*, whereas *Zaglossus bruijni* crania appear to have specialisations superimposed on these basically size-related differences in snout morphology. There is a relative increase in snout length, increased narrowness of the rostrum and a greater degree of downward curvature of the beak that must relate solely to habitus.

In a recent paper (Murray, 1978) I tentatively assigned the specimen Z.2031 to *Zaglossus robusta*. Having inspected more material I am now aware that the associated humeri of the Montagu skeleton are clearly conspecific with *E. ramsayi*. However, the great similarity of the crania indicate that *E. robusta* and *E. ramsayi* must either be closely related species or represent a temporal cline of the same species (Fig. 10).

While there is nothing to exclude the unique features of the *O. maximus* humerus from being valid specific characteristics, it is possible that the tapered entepicondyle is due to individual variation of an inherently variable structure. Similarly, the large posterior opening of the entepicondylar foramen may be an individual variation or it may change with increasing age (as is the tendency of many major foramina, especially among long-lived mammals).

Since there is no solid evidence to indicate that the humerus is representative of a unique tachyglossid species, the association of the humerus with the *E. robusta* cranium supports Dun's diagnosis. If the species is indeed somewhat older than

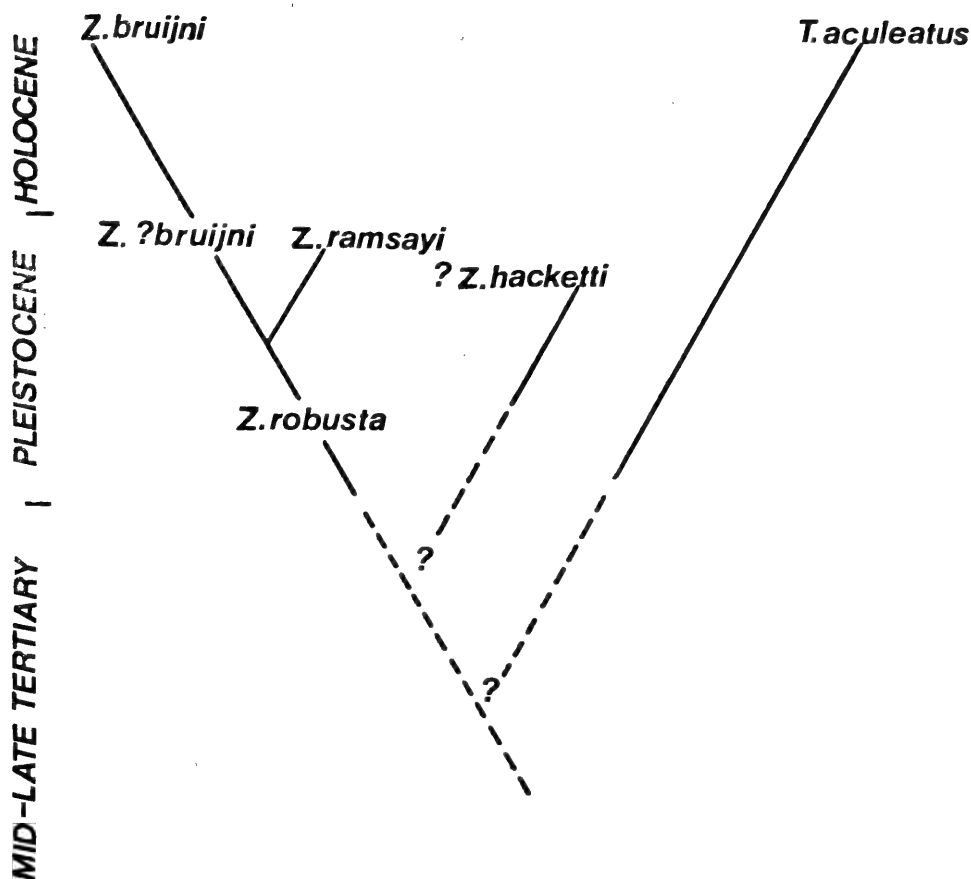


FIG. 11.—Dendrogram depicting one possible set of relationships of late Cenozoic tachyglossid genera and species. *Tachyglossus* is less specialised than any *Zaglossus* species suggesting early dichotomous branching of the two genera. The stem form for both genera therefore may have resembled *Tachyglossus* more than *Zaglossus*. The relationships within *Zaglossus* are close, probably more linear than branching. *Z. robusta* may have been ancestral to *Z. ramsayi* which gave rise to *Z. bruijni* in the upper Pleistocene. "*Zaglossus*" *hacketti* is *Incertae sedis*, shown here as an errant line from the base of the *Zaglossus* lineage. Time of branching is entirely speculative.

FOSSIL ECHIDNAS

E. ramsayi it is almost certainly ancestral to that species and possibly to *Zaglossus bruijni* also. However, the scarcity and apparent relatively late appearance of gracile remains in conjunction with certain morphological features suggest to me that *Z. bruijni* was derived from *E. ramsayi* in the upper, possibly very late Pleistocene (Fig. 11). Because I consider *E. robusta* to be ancestral to *Z. bruijni* via an intermediate form (*E. ramsayi*), I suggest that the genus *Zaglossus* be applied to these species.

Until more complete specimens of the gracile form become available for comparison, I suggest that the species *Z. bruijni* be reserved for the specialised end form from New Guinea.

It is possible, but rather unlikely, that the gracile material represents a typical morphological variant of *E. ramsayi*, alternatively it could represent an additional species having no closer relationship to *Z. bruijni* than the latter species. I therefore suggest *Zaglossus* cf. *bruijni* or *Zaglossus* sp. for the Australian late Pleistocene gracile form.

Zaglossus hacketti differs substantially from both fossil and living representatives of *Zaglossus* as defined here (Table 5) and from *Tachyglossus*.

SYSTEMATICS

SUBCLASS PROTOTHERIA ORDER MONOTREMATA FAMILY TACHYGLOSSIDAE

Zaglossus ramsayi Owen 1844

1868 *Echidna owenii* Krefft, Ann. Mag. Nat. Hist. 4 (1) 113, 114, Figures 1-3 (*Nomen vanum*).

1884 *Echidna ramsayi* Owen, Phil. Trans. R. Soc., 175, 273-5, Pl. 14, Figures 1-3.

1887 *Echidna gigantea* Roger, Ber. Naturw. ver Schwaben, 29 (4).

1921 *Zaglossus harrissoni* Scott and Lord, Pap. Proc. R. Soc. Tasm., 13-15, Pl. 5.

Holotype—Fragmentary left humerus, Aust. Mus. F.10948.

Type locality—Wellington cave breccia, Wellington Caves, N.S.W.

Age—Pleistocene.

Referred material—Right femur Aust. Mus. F.10888, Wellington cave breccia; right femur, Aust. Mus. F.13580, Wellington cave breccia; left humerus South Aust. Mus. P18602, Henschke's Quarry Cave, Naracoorte, S.A.; left femur South Aust. Mus. P18576, Henschke's Quarry Cave, Naracoorte, S.A.; right femur Queens Victoria Museum 1965:39:5, Egg Lagoon, King Island; cranium, vertebrae, innominate, humeri, scapulae, femora, tibiae, fibulae, clavicles and episternum (associated), Tasm. Mus. Z.2031, Montagu Caves, Tasmania.

P. F. MURRAY

Zaglossus robusta Dun 1895

1895 *Echidna* (*Proechidna*) *robusta* Dun, Rec. Geol. Surv. N.S.W. 4, 121-3, Pl. 12, Figures 5, 6.

1895 *Ornithorhynchus maximus* Dun, Rec. Geol. Surv. N.S.W. 4, 123-5, Pl. 11. Figures 1-2.

Holotype—Cranial fragment Aust. Mus. F.51451, atlas F. 51452.

Type Locality—Canadian Deep Lead Mine, Gulgong goldfield, N.S.W.

Age—Pliocene.

Referred specimen—right humerus Aust. Mus. F.51453, "*Ornithorhynchus maximus*", Canadian Deep Lead Mine, Gulgong goldfields, N.S.W.

Zaglossus hacketti probably requires generic revision. Its alignment with *Zaglossus* is no more satisfactory than placing the species in *Tachyglossus*. Therefore I suggest that until the material can be re-examined in detail and compared with new specimens of both fossil and living *Zaglossus* that it be referred to as "*Zaglossus*" *hacketti*.

It can be concluded that there are three extinct species of tachyglossid and tentatively two genera:

Zaglossus robusta Pliocene

Zaglossus ramsayi Pleistocene

"*Zaglossus*" *hacketti* Pleistocene.

Surviving or possibly surviving species found as fossils in the late Pleistocene include:

Zaglossus cf. *bruijini* (Nombe Rock Shelter)

Zaglossus sp. (Naracoorte Caves)

Tachyglossus cf. *aculeatus*,

making a total of five to six species and three genera ranging from possibly Pliocene to Recent.

FUNCTIONAL MORPHOLOGY

The differences in morphology between *Zaglossus ramsayi* and *Zaglossus bruijini* may relate primarily to diet and feeding behavior. The shorter, broader, less downcurved beak and very compact long bones with more prominent flanges and lever arms for muscular attachment probably enabled *Z. ramsayi* to pry up sizeable logs and stones and to tear into resistant materials such as rotten wood and termite's nests. Their feeding behavior may have been similar to that of *Tachyglossus* but on a grander scale.

The long, slender downcurved rostrum of *Zaglossus bruijini* is not shaped for effective prying and lifting. The snout is an adaptation for probing straight down

into the substrate from a normal quadrupedal stance. The humeri of *Zaglossus bruijni* are comparatively slender with less development of the processes to which the rotator cuff musculature is attached. Thus while *Z. bruijni* is probably a reasonably good digger, by inference, *Z. ramsayi* was much more efficient.

Van Deusen and George (1969:15) report that *Zaglossus bruijni* is fond of earthworms and that this food is found in good supply in their habitat. This food preference has been confirmed by the observations of G. Hope and M. Griffiths (pers. comm.). Their descriptions of the feeding behavior of *Zaglossus bruijni* fit the morphology. *Zaglossus bruijni* probes the soft humus layers with its long beak, inserting the tongue and retracting it through a high density of earthworms. Both the mossy floor of the cloud forests and the damp, alpine turf, where long-beaked echidnas are sometimes seen contain a great abundance of earthworms (Van Deusen and George, 1969; Hope and Hope, 1976).

"*Zaglossus*" *hacketti* may have had locomotor and postural differences from both *Tachyglossus* and *Zaglossus*. One possible postural correlate of the shortened tibia and relatively long femur is an adaptation to shift the center of gravity of body mass backwards. This may have allowed mobility of the forelimbs for digging or tearing and may have permitted the animal to easily assume an assisted bipedal stance while feeding on ants or termites nests, a posture sometimes used by both living genera (Brattstrom, 1973; Van Deusen and George, 1969).

EXTINCTION

Extinction of the genus *Zaglossus* in Australia probably occurred during the late Pleistocene, possibly long before New Guinea was isolated from the Australian mainland by the Torres Strait. In a technical sense therefore, *Zaglossus* did not become extinct on the continent until well into the Holocene. However, the species *Z. bruijni* appears to have remained confined to the montane regions of New Guinea at least since the end of the Pleistocene. *Zaglossus bruijni* habitat includes montane forest to alpine grasslands at altitudes of between 1800 and 4000 metres (Hope and Hope, 1976). Late Pleistocene Australian *Zaglossus* habitat appears to have been sparsely forested grassland or mosaic savanna where they lived in association with both browsing (*Sthenurus*, *Palorchestes*) and grazing (*Macropus* spp., *Protemnodon* spp.) herbivores. *Zaglossus bruijni* has survived intense hunting pressure in New Guinea for at least 26,000 years. It seems unlikely therefore that man was directly responsible for the disappearance of the genus in Australia.

It is possible that the Australian *Zaglossus* species were dependant on large ecotonal habitats; as were many other large mammals. The balance of glassland to forest edge may have begun to change toward the end of the glaciation. Depending on local and regional climatic factors, broad, ecotonal habitats may have given way to more highly differentiated plant formations: either more open (warming, high evaporation) or more thickly forested (warming, low evaporation or increased precipitation). The resulting sparse or highly varied plant formations could

not support a high biomass consisting of closely related species. Intense competition within the community would result in extinctions and stringent selection favouring the survival of smaller species within a family through the postglacial maximum and into the Holocene. Reduction of habitat suitable for the large entomophagous Australian *Zaglossus* may have favoured population increases in *Tachyglossus*. The species is present, but not as common as *Zaglossus* in late Pleistocene deposits. The local demise or reduction in numbers of *Zaglossus* allowed *Tachyglossus* to invade habitats that were previously marginal to it due to competition.

In New Guinea, *Zaglossus* survived the end of the last glaciation by following a narrow band of suitable habitat up and down the vertically zoned mountains. The worm feeding specialisation may have contributed to the survival of these populations, but it is equally possible that the worm feeding adaptation has evolved since the glacial maximum when populations may have become isolated by the elevation of suitable habitat due to increasing temperature.

SUMMARY AND CONCLUSIONS

Fossil *Zaglossus* material has been recovered from cave and swamp deposits in all Australian states. There were three separate species dating from the late Cenozoic that became extinct by the end of the last (Wisconsin) glaciation. These include *Zaglossus robusta* Dun, *Zaglossus ramsayi* Owen and "*Zaglossus*" *hacketti* Glauert. A slender or gracile form resembling *Zaglossus bruijni* is also present in the Australian late Pleistocene. *Zaglossus bruijni* probably evolved from *Z. ramsayi* in the late Pleistocene. *Z. bruijni* was able to survive ecological changes that commenced after the glacial maximum due to the vertical zonation of life zones in the montane regions of New Guinea. The species appears to have become specialised for eating worms by probing in the soft moist substrate with its long, curved beak. The time of origin of this specialisation is unknown. It may have commenced with the isolation of *Zaglossus* populations in the New Guinea highlands or perhaps the species arose earlier and had spread to all suitable habitats before becoming extinct everywhere except New Guinea. *Zaglossus robusta* and *Zaglossus ramsayi* were probably entomophagous echidnas that used their more powerful forelimbs and comparatively broad, straight beaks for low angle probing and prying, digging and tearing of termites' and ants' nests.

"*Zaglossus*" *hacketti* was an extremely large species. It may have attained nearly twice the length of *Zaglossus bruijni*. Morphological differences in the limb bones indicate that this echidna had locomotor and postural differences from both *Tachyglossus* and *Zaglossus*. "*Zaglossus*" *hacketti* should be given separate generic status.

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Abbreviations of museums referred to in text:

A.M.;	Aust. Mus.	Australian Museum, Sydney, N.S.W.
S.A.M.;	S. Aust. Mus.	South Australian Museum, Adelaide, S.A.
W.A.M.		West West Australian Museum, Perth, W.A.
T.M.		Tasmanian Museum, Hobart, Tas.
Q.V.M.		Queen Victoria Museum, Launceston, Tas.
AMNH		American Museum of Natural History, New York, U.S.A.

Monotreme Haemoglobin and Myoglobin Amino Acid Sequences and Their Use in Phylogenetic Divergence Point Estimations

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ABSTRACT

Many of the amino acid sequences of the globin chains of the echidna and platypus have been determined.

These sequences have been used to investigate the concept that homologous proteins evolve at a constant rate which is independent of species. Constancy of rate would allow divergence date estimates to be made directly by measuring amino acid differences between chains.

The relative rates of myoglobin, α - and β -globin chain mutation were determined and this data used with the monotreme sequences to give three independent estimates of the dates of divergence of the monotremes from the marsupials and eutherian mammals. The dates obtained vary markedly and the concept of constant protein evolutionary rate is not supported.

INTRODUCTION

The amino acid sequences of the α - and β -chains from the major haemoglobins of the echidna (Whittaker *et al.*, 1972, 1973; Dodgson *et al.*, 1974), and of the platypus (Whittaker and Thompson 1974, 1975), as well as the myoglobin from both animals (Fisher and Thompson 1976; Castillo *et al.*, 1978) have been determined. This represents the sequencing of all of the major globin chains of the two monotremes.

The use of amino acid sequences of proteins in evolutionary studies was suggested by Crick (1958) when he argued "that these sequences are the most delicate expression possible of the phenotype of an organism and that vast amounts of evolutionary information may be hidden away within them". Zuckerkandl and Pauling (1962) showed how such calculations could be made, although only limited data was available at that time. Since then many sequences have been determined (Dayhoff, 1972), predominantly on relatively simple proteins from mammalian sources. Such studies have resulted in the detection of a number

of examples of gene duplications both to give larger genes or to give rise to two independent genes with varying functions (Fitch and Margoliash, 1970). This has led to reconstruction of ancestral sequences and construction of gene and species phylogenies (Goodman *et al.*, 1971; Dayhoff, 1972). Of particular interest is the concept of a constant rate of mutation of proteins independent of species (Kimura, 1969; Wilson and Sarich, 1969; Dickerson, 1971). Constancy would allow estimation of divergence dates to be made simply by determination of the number of amino acid differences between homologous proteins in the two species being compared. Air *et al.* (1971) used myoglobin and α - and β -globin chain sequences to obtain three independent estimates of the marsupial-eutherian divergence date. Although the sample sizes were small (5 myoglobin, 8 α - and 6 β -globins), the results were consistent with statistically constant mutation rates for each of the three proteins and with the time of divergence indicated by palaeontology. These results prompted the determination of the amino acid sequences of monotreme globins in an attempt to resolve the controversy surrounding the origins and affinities of this group.

MATERIALS AND METHODS

A computer programme was used to compare amino acid sequences over 156 positions, using the sequences with gaps as listed in Dayhoff (1972, 1973, 1976).

The palaeontological estimates of dates of divergence were taken from Romer (1966) and Romero-Herrera *et al.* (1973) and are listed in Table 1.

The method of calculation is basically similar to that of Air *et al.* (1971) and Thompson and Air (1971), with a modification (Dayhoff, 1972) which allows for the possibility that more than one mutation may have occurred at a particular site. To establish the mean rate of protein evolution, the known sequences of each globin chain are compared and the number of amino acid differences determined—Tables 2, 3 and 4 upper triangles. A 10% difference in sequence cut-off was applied so that closely related groups which have

TABLE 1
PALAEOONTOLOGICAL ESTIMATES OF DATES OF DIVERGENCE

DIVERGENCE POINT	ESTIMATED TIME OF DIVERGENCE (million years)
Shark—bony fish, amphibians, reptiles, birds, mammals	440 ^A
Carp—amphibians, reptiles, birds, mammals	425 ^A
Newt, frog—reptiles, birds, mammals	350 ^A
Chicken, viper—mammals	295 ^A
Chicken—viper	280 ^A
Marsupials—eutherian mammals	104 ^B
General Radiation of Eutherian Mammals	68 ^B
Horse—bovine	55 ^B
Human, squirrel monkey—lemur, galago	52 ^B
Human—squirrel monkey	30 ^B
Lemur—galago	18 ^B
Badger—seal, sea lion	45 ^A
Seal—sea lion	23 ^A

Sources: A. Romer (1966); B. Romero-Herrera *et al.* (1973).

TABLE 2
MATRICES OF DIFFERENCES BETWEEN MYOGLOBINS

The matrix of observed amino acid differences between myoglobin sequences, compared over 156 residues, is shown in the upper triangle. PAM units per 100 amino acids compared are shown in the lower triangle.

	HUMAN	SQUIRREL MONKEY	LEMUR	GALAGO	HEDGE HOG	BADGER	HORSE	OX	DOLPHIN	SEAL	SEA LION	RED KANGAROO	OPOSSUM	ECHIDNA	PLATYPUS	CHICKEN
HUMAN																
SQUIRREL MONKEY	12															
LEMUR	16	12														
GALAGO	17	17	15													
HEDGE HOG	11	13	15	16												
BADGER	12	13	13	18	13											
HORSE	13	13	8	15	13	12										
OX	22	23	17	23	23	19	14									
DOLPHIN	16	21	14	20	20	18	12	19								
SEAL	18	20	12	21	17	14	15	21	14							
SEA LION	14	14	13	16	15	12	13	23	16	12						
RED KANGAROO	15	15	16	20	17	15	18	27	20	20	15					
OPOSSUM	11	14	17	20	14	15	16	26	21	20	15	10				
ECHIDNA	19	20	17	19	20	23	17	29	20	20	20	16	15			
PLATYPUS	19	19	16	18	19	21	19	29	21	19	18	17	14	6		
CHICKEN	28	32	31	31	29	32	28	38	31	31	30	27	30	31	30	

TABLE 3

MATRICES OF DIFFERENCES BETWEEN α -CHAINS

The matrix of observed amino acid differences between α -chain sequences compared over 143 residues is shown in the upper triangle. PAM units per 100 amino acids compared are shown in the lower triangle.

	HUMAN	MOUSE	DOG	RABBIT	HORSE	OX	GREY KANGAROO	OPOSSUM	ECHIDNA IB	ECHIDNA IIA	PLATYPUS	CHICKEN	VIPER	NEWT	CARP	SHARK
HUMAN																
MOUSE	18															
DOG	23	25														
RABBIT	25	26	27													
HORSE	27	27	28	25												
OX	24	24	25	18	17											
GREY KANGAROO	27	28	29	20	23	21										
OPOSSUM	33	33	34	32	38	39	42									
ECHIDNA IB	33	34	35	48	38	39	60	49								
ECHIDNA IIA	37	37	38	46	38	40	64	7	12							
PLATYPUS	40	40	41	42	38	40	62	12	17	17						
CHICKEN	42	42	43	39	35	33	62	45	49	43	43					
VIPER	46	46	47	50	49	52	79	72	74	67	57	57				
NEWT	49	49	50	79	74	70	76	83	83	78	85	85	85			
CARP	53	53	54	87	78	76	87	95	91	93	91	91	91	95		
SHARK	57	57	58	93	95	93	104	110	116	104	113	113	113	119	122	

TABLE 4

MATRICES OF DIFFERENCES BETWEEN β -CHAINS

The matrix of observed amino acid differences between β -chain sequences, compared over 146 residues, is shown in the upper triangle. PAM units per 100 amino acids compared are shown in the lower triangle.

	HUMAN	MOUSE	DOG	RABBIT	HORSE	OX	GREY KANGAROO	POTOROO	ECHIDNA	PLATYPUS	CHICKEN	FROG	SHARK
HUMAN													
MOUSE	21												
DOG	11	24											
RABBIT	10	22	16										
HORSE	19	31	24	19									
OX	19	34	22	24	24								
GREY KANGAROO	33	41	29	32	38	39		15	39	40	47	68	91
POTOROO	37	42	29	33	37	44	11		35	37	45	66	90
ECHIDNA	25	33	25	25	29	33	34	29		14	42	60	91
PLATYPUS	28	37	31	27	28	36	35	32	10		42	64	91
CHICKEN	41	45	37	44	43	53	43	41	37	37		66	87
FROG	64	61	61	59	65	69	74	70	61	67	70		90
SHARK	130	127	133	127	133	133	127	124	127	127	115	124	

many extant members and/or have been particularly popular with sequencers (e.g. the primate group) did not unduly influence the calculation of the mean rate.

The amino acid differences are normalised to the number of differences per 100 residues compared and the formula of Dayhoff (1972) applied to allow for possible multiple mutations. This gives "accepted point mutations" (PAM units) per 100 residues compared, as shown in the lower triangles of Tables 2, 3 and 4.

Protein evolutionary rates per arm (r) are determined from comparisons that do not involve monotreme sequences by the formula $r = \frac{1}{2} \frac{\text{PAM}}{t}$ where t is the relevant palaeontological estimate of divergence date as shown in Table 1.

Mean rates of protein mutation in terms of PAM units per 100 residues per arm per million years were obtained by averaging the r values (these are reciprocals of the Y values of Air *et al.* (1971)) for all possible comparisons.

Dates of divergence of monotremes from other mammals were computed using the mean " r " values and the number of amino acid differences between the monotremes and the other mammalian species (Tables 2, 3 and 4).

RESULTS

A summary of the major features of the structure of monotreme haemoglobin and myoglobin is presented in Table 5—the comparison is made against human globin chains.

The most notable feature of the chains is their conserved nature. Although there is 16-28% difference in sequence from the human chains, chain length and most of the important functional sites are unaltered (Perutz, 1969, 1976). The four changes in haem contact sites are conservative, with the two myoglobin changes being observed in other species. The two α -haem contact changes, while

TABLE 5
STRUCTURAL SUMMARY OF THE MONOTREME GLOBINS
COMPARED WITH HUMAN GLOBINS

- (a) All globin chains of the usual length
i.e. myo- 153 α -141 β -146
- (b) Number of amino acid differences from corresponding human globin
- | | | | |
|----------|-----|------------|-----------|
| | Myo | α - | β - |
| Echidna | 25 | 37 | 31 |
| Platypus | 25 | 39 | 34 |
- (c) Important Contact Sites are Preserved.
Haem contacts (Perutz, 1976)
- (i) Myo-haem: 2 changes in 14 sites
 - G4 Tyr \rightarrow Phe (also in marsupials)
 - E10 Thr \rightarrow Val (echidna and horse only)
 - (ii) α -haem: 2 changes in 16 sites
 - CD4 Phe \rightarrow Met (echidna only)
 - E10 Lys \rightarrow Arg (echidna IA & IB only)
 - (iii) β -haem: no change in 16 sites
- α_1 - β_0 Contact sites—identical in platypus and echidna
—changed from human in α CD2
Pro \rightarrow Ser in both animals
- (d) No change in 2,3 diphosphoglycerate binding sites or in residues involved in the alkaline Bohr (H^+ binding) effect.

Differences in Echidna α -chains

Position	HbIA	HbIB	HbIIA
A5	Lys	Lys	Arg
A10	GLY	SER	Ser
B4	Glu	Glu	Asp
E3	Gln	Gln	His
E5	Lys	Lys	Arg
E10	Arg	Arg	Lys
E19	Ala	Ala	Val
EF7	ASN	SER	Gly
F3	Ala	Ala	Asp
G9	SER	ALA	Ala
GH3	GLU	ALA	Glu

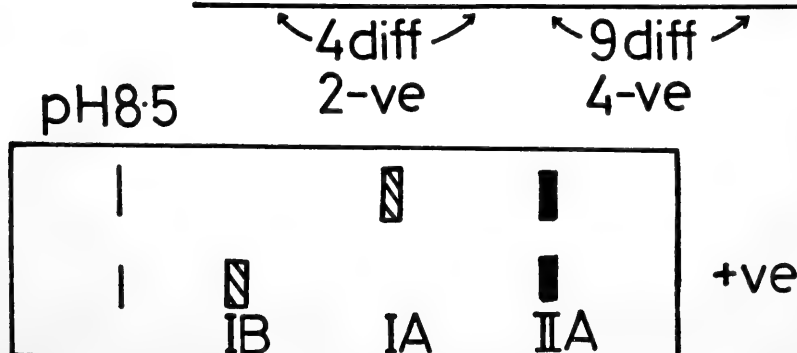


FIG. 1.—Amino acid differences in echidna α -globins and relative electrophoretic mobility of echidna haemoglobins at pH 8.5.

unique to the echidna, maintain the nature of the contact sites and possibly have little effect on stability or haem-haem co-operativity.

The conservation and the similarity of the $\alpha_1\beta_2$ contact, 2,3- diphosphoglycerate binding sites and the amino acids involved in the alkaline Bohr (H^+ binding) effect is somewhat surprising considering the different life styles of the two animals and the measured differences in their oxygen saturation profiles. The echidna haemoglobin is 50% saturated at a partial pressure of 12 mm, while the platypus haemoglobin P_{50} occurs at 18 mm (Hosken, 1978). This difference could possibly be due to differing levels of erthrocyte 2,3-diphosphoglycerate, which has not as yet been measured.

The echidna possesses major and minor haemoglobins, and both haemoglobins exhibit polymorphic forms (Cooper *et al.*, 1973). The amino acid sequences of two of the major haemoglobins, HbIA and HbIB, have been determined (Dodgson *et al.*, 1974; Whittaker *et al.*, 1973), as well as one of the minor haemoglobins, HbIIA (Thompson *et al.*, 1973). In all haemoglobins the variation in sequence was confined to the α -chain. The differences detected, together with a diagrammatic representation of their mobility on electrophoresis at pH 8.5, are shown in Figure 1. HbIA has two extra negative charges (there are two α chains in the tetramer) compared with HbIB, due to the substitution of glutamic acid for alanine at position GH3. HbIIA also has this change at GH3 and thus has a further two negative charges due to the change of aspartic acid for alanine at position F3. The platypus also has multiple haemoglobins, with three different forms being detected by ion exchange chromatography (Whittaker and Thompson, 1974). The source of the variations remains to be investigated.

When differences in amino acid sequences are used for evolutionary rate calculations (Tables 2, 3, 4) the mean values of r obtained were: myoglobin 0.108 ± 0.011 ($n=92$); α -chain 0.115 ± 0.007 ($n=92$); β -chain 0.133 ± 0.012 ($n=60$). Limits are 95% confidence intervals for the means.

The narrowness of the confidence intervals is suggestive of constancy of evolutionary rate. However, when monotreme divergence date calculations are carried out using these rates and the comparisons involving the monotreme

TABLE 6
ECHIDNA-PLATYPUS DATES OF DIVERGENCE
(millions of years B.P.)

	Myo	α	β -
Echidna IB-Echidna IIA	—	30	—
Echidna-Platypus	28	52 ^{IB}	38
Monotreme-Marsupial	72	234	122
Monotreme-Placental	93	171	112

Abbrev.: IB indicates divergence was calculated with IB variant of echidna.

MONOTREME GLOBINS AND PHYLOGENY

sequences, three varying estimates of the date of divergence from other mammals are obtained:

myoglobin 90 ± 16 million years ($n=26$);
 α chain 186 ± 38 million years ($n=24$); and
 β -chain 114 ± 15 million years ($n=16$);

limits are ± 1 S.D. Clearly at least one of the chains in both monotremes has mutated at a non-average rate. A complete list of divergence dates estimated from monotreme sequence data is presented in Table 6.

Rate variability between chains of different type is evident in comparisons of species for which all three globin chain sequences are known (Table 7). This comparison, which is independent of palaeontological derived data, indicates variability in rates of up to 2.7 times for myoglobin chains and 1.8 times for β -chains relative to α -chains.

TABLE 7

VARIABILITY OF MUTATION RATE BETWEEN CHAINS

Comparison of the amino acid differences for species in which all three chains have been sequenced (comparison against human globins)

	Myo	α -	β	Myo/ α	β/α
Horse	18	18	25	1.00	1.39
Ox	29	17	25	1.71	1.47
Kangaroo	20	27	38	0.74	1.41
Echidna	25	37	31	0.68	0.84
Platypus	25	39	34	0.64	0.87
Chicken	25	35	45	1.00	1.29

Variability within like chains can be shown by comparing sequences in groups of three. Balancing the number of amino acid differences observed between the major and minor α -chain of the platypus indicates that the minor chain has mutated at five times the rate of the major chain (Figure 2). Comparisons of kangaroo, opossum and human α -chains (Figure 3) indicate twice the rate in the opossum arm. This type of variation is not uncommon and other examples can be selected from the data presented in Tables 2, 3 and 4.

It is not possible to obtain simple mathematical balances when more than three species are compared. Various methods of phylogenetic tree building based on apportioning differences (Fitch and Margoliash, 1970; Dayhoff, 1972; Moore *et al.*, 1973; Romero-Herrera *et al.*, 1973) all indicate mutational rate variability of the order shown in Figures 2 and 3.

Recalculation from the present sequence data (Tables 2, 3 and 4) and the mean r values gave marsupial-placental divergence dates of:

myoglobin 81 million years
 α -globin 144 „ „
 β -globin 136 „ „

VARIATION IN MUTATION RATES

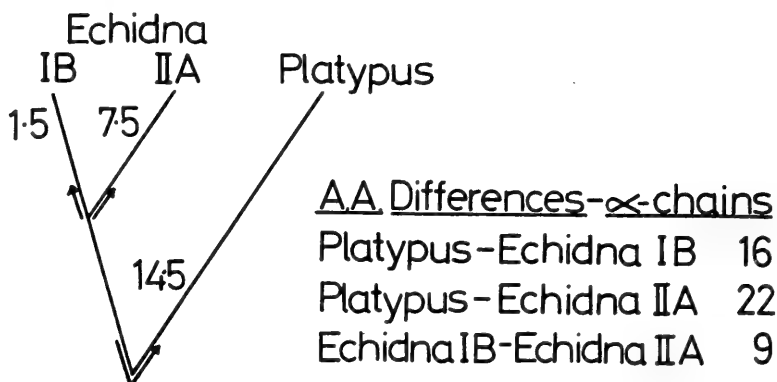


FIG. 2.—Mutational rate variation between the α -chains of the major and minor haemoglobin of the echidna. Numbers are assigned to each arm to balance the observed number of sequence differences.

VARIATION IN MUTATION RATES.

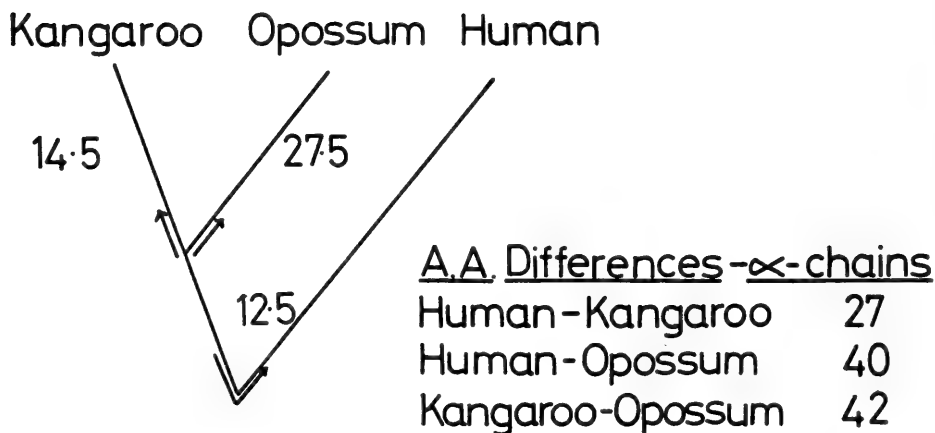


FIG. 3.—Mutational rate variation between the α -chains of the kangaroo and the opossum. Numbers are assigned to each arm to balance the observed number of sequence differences.

MONOTREME GLOBINS AND PHYLOGENY

There is less consistency here than was obtained earlier by Air *et al.* (1971), when fewer sequences were available, and poor agreement with the 104 million years (Table 1) estimate used in the calculation of the r values.

DISCUSSION

It is apparent that, although in general the number of amino acid differences between sequences increases with evolutionary distance, there is insufficient constancy of the mutational rate to allow accurate divergence date estimates to be made directly from the sequence data.

Table 6, which summarises the constant rate calculations, illustrates this last point all too clearly. The method does not give a reasonably consistent estimate of the monotreme divergence date and can not help resolve the question of the origins of the monotremes. Calculations using myoglobin differences indicate a divergence off the marsupial line, while α - and β -globin calculations indicate a closer affinity with the placental mammals.

This somewhat disappointing result is not improved by consideration of minimum nucleotide changes required to give the observed sequence differences or by attempting to reconstruct ancestral sequences. Protein taxonomy is, at present, more suited for fine resolution between closely related species, e.g. the work of Romero-Herrera *et al.* (1973) on monkey myoglobins.

The problems of determining dates of divergence and affinities of groups more distantly related may be overcome when the amino acid sequences of a large number of proteins from the animals being compared becomes available. There are in the order of 10^5 to 10^6 protein chains in a mammal. Possibly the greater "sample size" would overcome the variability of the individual proteins that is illustrated in the results obtained with monotreme globins.

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Adaptations of Monotreme Lactate Dehydrogenases to Temperature

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ABSTRACT

Studies on the thermal properties of lactate dehydrogenases of monotremes are reviewed to demonstrate mechanisms by which these enzymes are adapted to function at body temperatures that are low and variable relative to those of most other mammals. These adaptations include (1) ΔG^\ddagger characteristics that enable high reaction rates to be achieved at lower temperatures; (2) weak-bond structural interactions that permit satisfactory enzyme-ligand binding at lower temperatures; (3) mechanisms for stabilizing reaction rates during rapid fluctuations in body temperature. It is concluded that lactate dehydrogenases of monotremes have been finely tuned to operate efficiently under the specific thermal environment encountered in these animals, and that there is little reason to consider that enzymes of monotremes suffer any disadvantages, relative to those of other mammals, because of this thermal environment. This conclusion does not support the view that the maintenance of a higher and more stable body temperature in most placentals and marsupials is an adaptation primarily for "optimising" the catalytic and regulatory properties of enzymes.

Studies on the thermal properties of enzymes from a wide range of animals have revealed adaptive mechanisms by which catalytic and regulatory properties can be maintained in the face of markedly different and often rapidly fluctuating temperatures (see Hochachka and Somero, 1973).

The purpose of this paper is to bring together a number of studies on the effects of temperature on lactate dehydrogenases of monotremes and to discuss the ways in which these enzymes are adapted to function at body temperatures that are low and variable relative to those of most other mammals.

EFFECTS OF TEMPERATURE ON ENZYME CATALYSED REACTIONS

The effects of temperature on enzyme catalysed reactions can be divided into two general classes: 1. rate effects, which determine how rapidly equilibrium is attained between substrates and products; 2. weak-bond structural effects, which influence those properties of the enzyme that depend upon non-covalent bonding. Examples of this second class are the binding of substrates and other ligands.

The effect of temperature on reaction rate is described by the Arrhenius equation:

$$k = Ae^{-E/RT}$$

where k is a rate constant, E the activation energy, R the gas constant, T the absolute temperature, and A is a constant.

Interpretation of the usually large effect of temperature on the rates of enzyme catalysed reactions (often 200-300% over a 3% change in absolute temperature) is based upon the concept of the formation of a high energy intermediate, the activated complex, which once formed decomposes to give products and free enzyme. The rate of the overall reaction is governed by the probability of forming the activated complex, and this probability depends upon the temperature of the

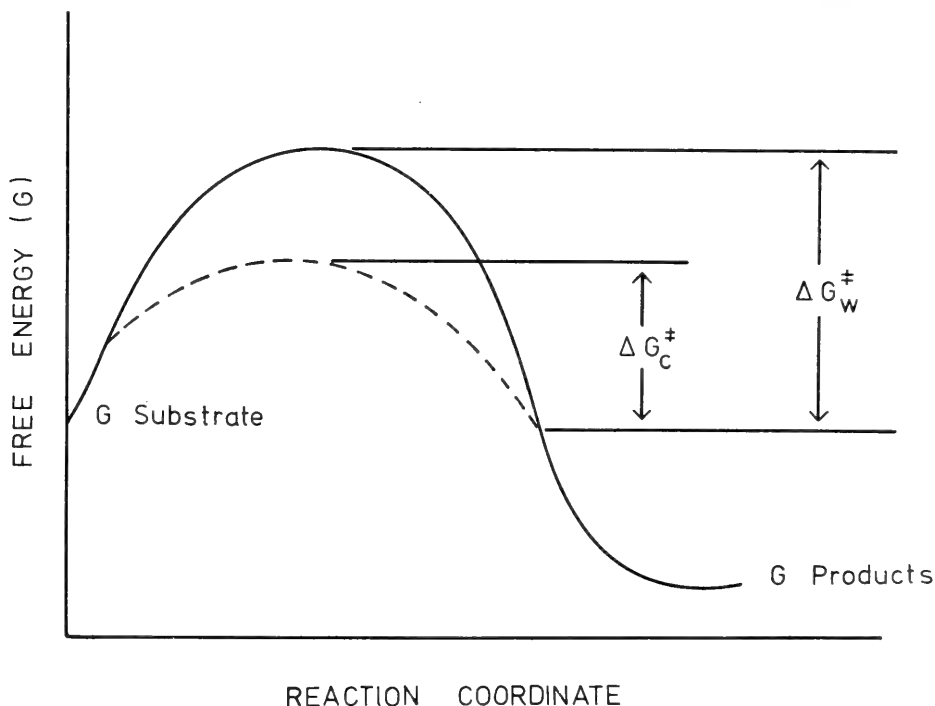


FIG. 1—Adaptation for maintaining high reaction rates at low cell temperature by reducing ΔG^\ddagger characteristics of enzymes from animals with low body temperatures.

ΔG^\ddagger_w = free energy of activation for an enzyme of an animal with a high body temperature.

ΔG^\ddagger_c = free energy of activation for a homologous enzyme of an animal with a low body temperature.

The enzyme from the animal with low body temperature is able to maintain higher reaction rates at a low temperature by significantly decreasing the energy 'barrier' to the reaction (ΔG^\ddagger).

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system, and the free energy difference between reactants and the activated complex (the Gibb's free energy of activation, ΔG^\ddagger). Thus at a given temperature the reaction rate is determined by the magnitude of ΔG^\ddagger . From the relationship between reaction rate and ΔG^\ddagger it would appear advantageous for reactions catalysed by enzymes of animals with low body temperatures to exhibit lower ΔG^\ddagger characteristics than the homologous reactions of animals with higher body temperatures. In this way high reaction rates could be maintained at low cell temperatures by using enzymes that are catalytically more efficient, that is enzymes with higher turnover numbers (amount of substrate converted/unit time/enzyme molecule). This idea of adapting to low temperatures by altering enzyme efficiency is represented diagrammatically in Figure 1.

The effects of temperature of weak-bond structural interactions can be summarized for the purpose of this discussion by stating that decreasing temperature tends to favour charge attractions and to disrupt hydrophobic interactions (Brandts, 1967).

From a consideration of these effects of temperature on enzyme catalysed reactions one might predict that enzymes from monotremes would display the following adaptive features: 1. ΔG^\ddagger characteristics that enable high reaction rates to be maintained at temperatures lower than those encountered in most other mammals; 2. weak-bond structural interactions compatible with function at these lower temperatures; 3. mechanisms for stabilizing reaction rates during fluctuations in body temperature. The extent to which these theoretically advantageous adaptations have been utilized can be assessed by comparing the thermal properties of enzymes from monotremes with those of homologous enzymes from other animals with markedly different body temperatures.

TABLE 1

ΔG^\ddagger VALUES AND TURNOVER NUMBERS OF LACTATE DEHYDROGENASE M_1 ENZYMES FROM ANIMALS WITH DIFFERENT BODY TEMPERATURES.

Animal	Body temp. (°C)	ΔG^\ddagger (cal/mol; 35°C)	Turnover No. ^d
Kangaroo	36	14010 ^a	3.1 x 10 ^{2a}
Echidna	23-32 ^c	13820 ^a	4.3 x 10 ^{2a}
Platypus	32	13660 ^a	5.6 x 10 ^{2a}
Possum	36	13325 ^a	9.8 x 10 ^{2a}
Rabbit	37	13250 ^b	1.1 x 10 ^{3b}
Chicken	42	13150 ^b	1.4 x 10 ^{3b}
Goanna	37 ^c	13350 ^a	9.0 x 10 ^{2a}
Halibut	10	12900 ^b	2.1 x 10 ^{3b}
Antimora	2	12710 ^a	2.7 x 10 ^{3a}

a. Data from Baldwin (1975)

b. Data from Low *et al.* (1973)

c. Body temperature of active animals

d. umoles NADH/min/mg protein, 35°C

RELATION BETWEEN ΔG^\ddagger AND BODY TEMPERATURE

Values of ΔG^\ddagger and turn over numbers calculated for purified lactate dehydrogenase M_4 enzymes of platypus, echidna, and a range of other animals with different body temperatures, are given in Table 1.

In general the ΔG^\ddagger values obtained for the enzymes of endotherms are higher than those of ectotherms, with the notable exception of the goanna lactate dehydrogenase which operates at a relatively high cell temperature in the active animal. However, among the endotherms it is clear that the magnitude of ΔG^\ddagger does not necessarily correlate with body temperature. For example, the lowest ΔG^\ddagger value is obtained for the chicken enzyme which functions at the highest temperature, while the values for the monotreme enzymes are higher than those of animals with body temperatures in the range 26° - 42° . Thus the question arises as to what factors, in addition to body temperature, might be involved in the selection of catalytic efficiency for a particular enzyme. The most obvious proposal is that the catalytic efficiency of any enzyme will be tuned to the particular metabolic requirements of the tissue in which it operates. The lactate dehydrogenase M_4 isoenzyme occurs in highest concentrations in white skeletal muscle. This tissue usually has a limited blood supply, little capacity for pyruvate oxidation, and a large fraction of energy for contraction is obtained from anaerobic glycolysis. Consequently the conversion of pyruvate to lactate is of greater importance in this tissue than in the more aerobic red skeletal muscles. As the levels of enzyme activity in tissues can be adjusted by changes in the catalytic efficiency as well as by altering the amount of enzyme, it might be argued that it would be of adaptive advantage for the ΔG^\ddagger values of lactate dehydrogenase M_4 to be lowered in species which depend to a greater degree on anaerobic glycolysis. To examine this proposal the levels of phosphorylase, myoglobin, and lactate dehydrogenase were determined in muscles of animals for which lactate dehydrogenase ΔG^\ddagger values are known. Phosphorylase is involved in the mobilisation of glycogen, and its maximum activity provides an index of the capacity of a muscle for anaerobic glycolysis (Crabtree & Newsholme 1972, Baldwin *et al.* 1977, Baldwin & Seymour 1977, Muller & Baldwin 1978). Myoglobin concentrations usually increase as reliance on anaerobic glycolysis decreases (Burleigh & Schimke 1968).

Some phosphorylase, myoglobin and lactate dehydrogenase levels are listed in order of decreasing lactate dehydrogenase M_4 ΔG^\ddagger values in Table 2. In each animal examined samples were taken from the palest skeletal muscle involved in bursts of rapid locomotion. For the animals with body temperatures in the range 36° to 42° , ΔG^\ddagger values decrease as the capacity for anaerobic glycolysis increases (increasing maximum activities of phosphorylase and lactate dehydrogenase, and decreasing myoglobin concentrations). The ΔG^\ddagger value for the echidna lactate dehydrogenase M_4 is lower than would be predicted from the enzyme activity and myoglobin data alone, but this low value can be interpreted as an adaptation for maintaining adequate reaction rates at body temperatures that are considerably below those encountered in the other endotherms.

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TABLE 2

CORRELATIONS BETWEEN LEVELS OF PHOSPHORYLASE, LACTATE DEHYDROGENASE AND MYOGLOBIN IN SKELETAL MUSCLE, AND LACTATE DEHYDROGENASE M_4 ΔG^\ddagger values

Tissue	Myoglobin (mg/g wet wt)	Phosphorylase ^a	LDH ^a	ΔG^\ddagger (cal/mole, 35°C)
Kangaroo thigh	4.7	26	227	14010
Echidna thigh	15.2	13	144	13820
Possum thigh	4.1	40	452	13325
Rabbit thigh	0.2	79	700	13250
Chicken pectoral	<0.2	83	1027	13150

a. umoles substrate/min/g wet weight muscle
Data from Baldwin (1975)

A major criticism of this interpretation of the correlation between ΔG^\ddagger values, temperature and levels of anaerobic glycolysis, is that lactate dehydrogenase M_4 catalyses a reaction close to equilibrium, and the activity of the enzyme in vertebrate muscle is always far in excess of the activities of phosphorylase and phosphofructokinase, both of which are considered to play a role in regulating glycolytic flux under anaerobic conditions in working muscle (Crabtree & News-holme 1972, Newsholme & Start 1973). In this situation it is difficult to understand why the catalytic efficiencies of lactate dehydrogenase M_4 in different species should be so finely tuned if its main function is in energy production during periods of muscle anoxia. Despite this objection, correlations clearly do exist between the maximum activity of lactate dehydrogenase and dependence on anaerobic glycolysis, both for homologous muscles from different species, and for different muscles within a single individual (e.g. Baldwin 1975, Baldwin & Seymour 1977, Muller & Baldwin 1978). If it is of advantage to an animal to regulate lactate dehydrogenase activity at this level, then the correlations between ΔG^\ddagger values, body temperature, and capacity for anaerobic glycolysis may well reflect selection for different catalytic efficiencies among lactate dehydrogenase M_4 enzymes from different organisms.

MAINTAINANCE OF WEAK-BOND STRUCTURAL INTERACTIONS AT DIFFERENT BODY TEMPERATURES

The binding interactions between enzymes and substrates involve weak, non-covalent bonds, and proceed with only small changes in free energy. As these bond energies are no more than an order of magnitude greater than the thermal energies present in organisms, it is not surprising to find that these weak-bond interactions have been subjected to stringent evolutionary selection, and that adaptive differences exist among homologous enzymes of animals with different body temperatures. This type of thermal adaptation is clearly demonstrated by the binding of oxamate to lactate dehydrogenase M_4 . Oxamate is isoelectronic and isosteric with the natural substrate pyruvate, and acts as a competitive inhibitor. During the binding of either

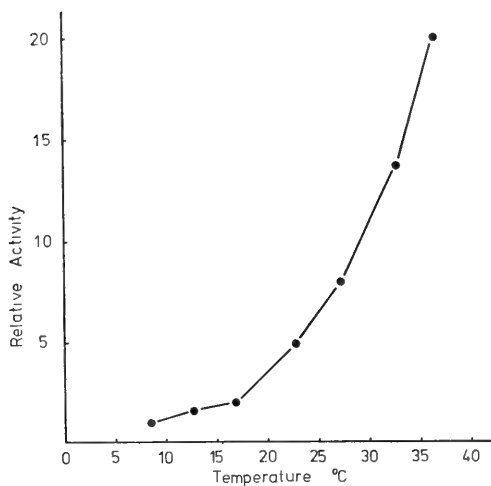


FIG. 2—Effect of assay temperature on the activity of lactate dehydrogenase M_4 from echidna with *saturating* concentrations of pyruvate and NADH (data from Baldwin and Aleksuk, 1973).

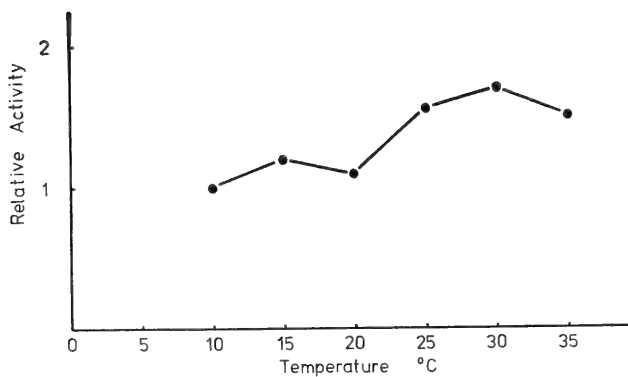


FIG. 3—Effect of assay temperature on the activity of lactate dehydrogenase M_4 from echidna with low concentrations of pyruvate and NADH approaching K_m levels (data from Baldwin and Aleksuk, 1973).

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oxamate or pyruvate, a negative charge must be neutralised and, because of the effect of temperature on charge attractions, the overall process should be favoured at low temperatures. If this binding interaction was identical in all homologs of the enzyme, then the lower the temperature the higher would be the affinity of the enzyme for oxamate or pyruvate. In this situation the enzyme from an animal with a low body temperature would have a higher affinity as this temperature than would the homologous enzyme from an animal with a higher body temperature, at its body temperature.

TABLE 3

EFFECTS OF ASSAY TEMPERATURE ON K_i OXAMATE FOR LACTATE DEHYDROGENASE M_4 ENZYMES OF ANIMALS WITH DIFFERENT BODY TEMPERATURES.

Animal	Body temp.	37°C	Body temp.
Ox	37	.19	.19
Possum	36	.19	.18
Platypus	32	.25	.18
Echidna	23-32	.29	.13-.18
Goanna	37	.19	.19
Antimora	2	.74	.19

Data from Hochachka *et al.* (1976)

The effects of assay temperature on the binding of oxamate by lactate dehydrogenase M_4 enzymes from a range of animals with different body temperatures are shown in Table 3. There are two main conclusions to be drawn from this data: (1) for a given enzyme, oxamate binding is influenced by temperature, with the affinity ($1/K_i$) increasing at lower temperatures as predicted from the effects of temperature on charge attractions; (2) despite this temperature sensitivity, the affinity for oxamate is very similar for each lactate dehydrogenase homolog when measured at the normal cell temperature encountered by the enzyme. It is clear that these enzymes have been adapted to function at this specific temperature. This relationship between ligand-binding ability and cell temperature has been observed with other enzymes, and reflects adaptive changes in weak-bond interactions involved in the binding process (Hochachka *et al.* 1975, Somero 1975). It appears that the echidna and platypus enzymes suffer no disadvantages in terms of enzyme-ligand affinities by functioning at cell temperatures considerably lower than those encountered by most placentals and marsupials.

STABILIZATION OF ENZYME REACTION RATES DURING FLUCTUATIONS IN BODY TEMPERATURE

Data obtained from echidnas in the field, in the laboratory, and in outdoor enclosures, indicate that the body temperatures of active animals generally lie within the range 23°-32°. During prolonged periods of low ambient temperature

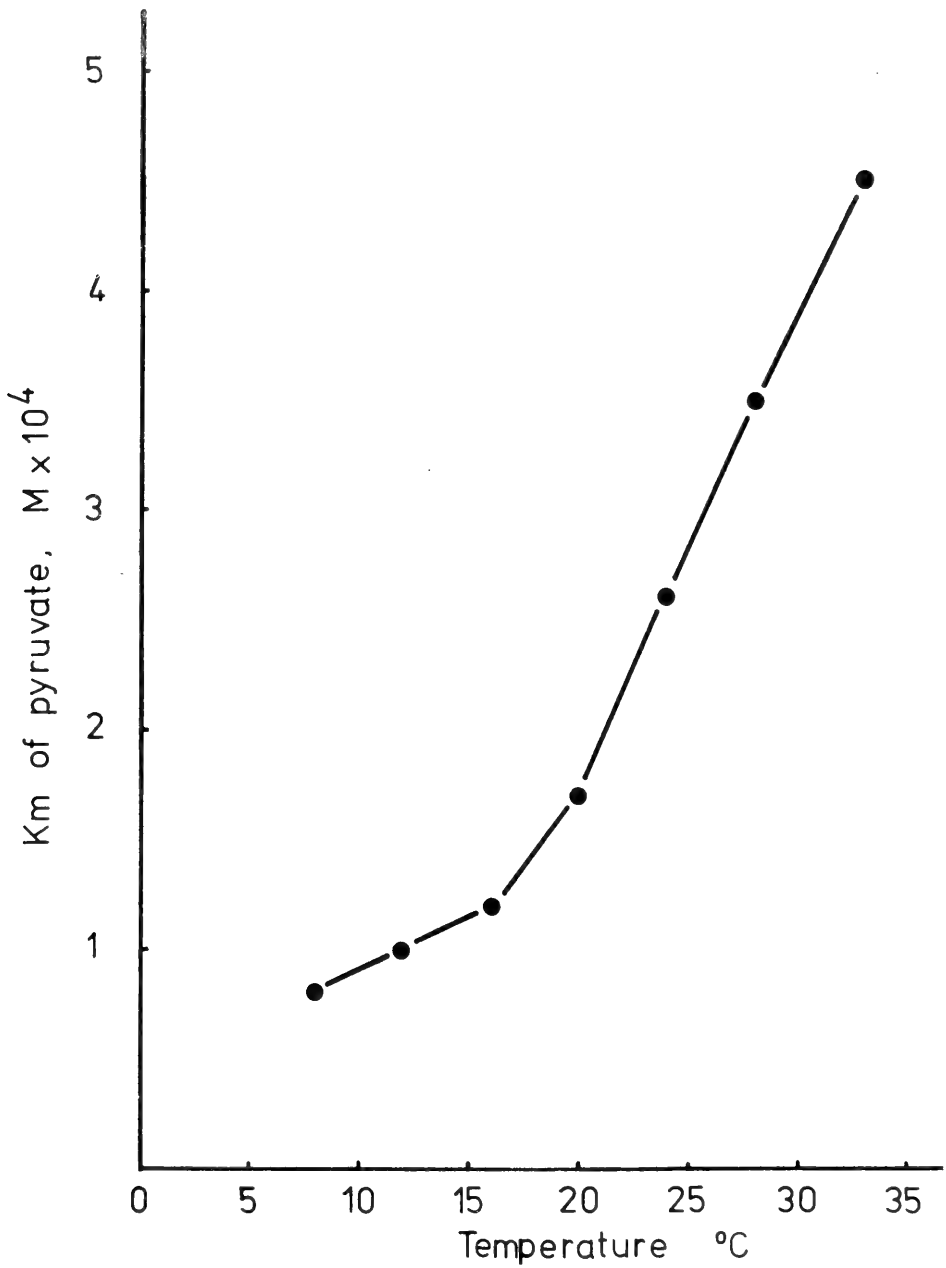


FIG. 4.—Effect of assay temperature on the apparent K_m of pyruvate for lactate dehydrogenase M_4 from echidna (data from Baldwin and Aleksziuk, 1973).

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echidnas may become torpid with body temperatures closely paralleling air temperatures down to at least 10° (Miklouho-Maclay 1883, Schmidt-Nielsen et al. 1966, Augee & Ealey 1968, Griffiths 1968, Augee et al. 1970). Such large fluctuations in body temperature might be expected to have detrimental effects upon the many physiological and biochemical processes that require relatively constant rates of enzyme catalysis.

When echidna lactate dehydrogenase M_4 is assayed over a range of temperatures at saturating levels of pyruvate and NADH, the reaction rate increases as temperature is raised, displaying a Q_{10} of 2-3 (Fig. 2). However, when the experiment is repeated at lower substrate concentrations approaching physiological levels (Fig. 3), the reaction rate is considerably less sensitive to temperature, with Q_{10} values approaching 1 over the thermal range normally encountered in active animals (23°-32°).

An explanation for this temperature insensitivity of reaction rates at low *in vivo* substrate concentrations is found in the effect of temperature on the weak-bond interactions involved in substrate binding. The relationship between enzyme-substrate affinity (as reflected by the apparent K_m pyruvate), and temperature, is shown in Figure 4. As expected, increasing temperature leads to the disruption of charge attractions and a subsequent fall in the affinity of the enzyme for pyruvate ($1/\text{apparent } K_m \text{ pyruvate}$). The adaptive significance of this phenomenon is thought to lie in the ability of these temperature induced changes in enzyme-substrate affinity to largely counteract the effects of fluctuating thermal energy upon reaction rates at low substrate concentrations approaching K_m values (Hochachka & Somero 1968, Baldwin & Hochachka 1970, Hochachka & Somero 1973). For example, while increasing temperature would be expected to increase reaction rates, as predicted by the Arrhenius equation, the concomitant fall in enzyme-substrate affinity acts to decrease reaction rates. In the reverse situation, the effects of decreasing temperature on reaction rate are offset by increasing enzyme-substrate affinity. In this way, relatively stable reaction rates can be maintained in the face of fluctuating cell temperatures.

CONCLUSIONS

The studies discussed in this paper show that lactate dehydrogenases of monotremes have been finely tuned to operate efficiently under the specific thermal environment encountered in these animals. Undoubtedly, similar thermal adaptations are common to other monotreme enzymes (for example, cytoplasmic malate dehydrogenase, Baldwin & Aleksuk 1973), and there seems little reason to consider that enzymes from these animals suffer any disadvantages, relative to those of mammals, because of the thermal environment in which they function. In the words of Barcroft (1934) — "nature has learned so to exploit the biochemical situation as to escape from the tyranny of a simple application of the Arrhenius equation." Such conclusions would not support the contention that the maintenance

of a higher and more stable body temperature in most placentals and marsupials is an adaptation primarily for "optimising" the catalytic and regulatory properties of enzymes.

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Adrenocortical Functions in Monotremes

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ABSTRACT

The structure of the adrenal gland of echidna and platypus is similar to that of birds or reptiles. The hormones secreted are the same as found in most vertebrates, although the platypus is peculiar in that the major glucocorticoid is cortisone. Secretion rates of echidnas are extremely low, while those of the platypus are similar to other mammals. The echidna survives adrenalectomy unless subjected to environmental stress. It is hypothesized that the role of glucocorticoids secreted by the echidna adrenal gland in response to stimulation by ACTH when the animal is subjected to a cold environment, is to synergise with ACTH in the mobilisation and utilisation of fat.

The secretions of the adrenal cortex influence many basic mechanisms essential for the survival of mammals in adverse environments. For this reason, investigation of adrenocortical functions in the prototherian mammals could be expected to shed some light on their metabolic organisation, particularly in relation to the mechanisms of adaptation to environmental disturbance.

Most of the information about adrenocortical function relates to the Tachyglossidae; in particular, to *Tachyglossus aculeatus*. The little information we have on that of *Ornithorynchus anatinus* suggests that there may be major differences between the two species. Firstly, if one takes adrenal size as an indicator of its possible importance in metabolic regulations, it is apparent that the adrenal gland of the echidna is the smallest, in relation to body mass, of all the mammals, while that of the platypus is comparable with that of eutherian and metatherian species (Table 1).

TABLE 1

ADRENAL GLAND WEIGHTS AS A FUNCTION OF BODY WEIGHT IN MAMMALS.

Non-therian (mean \pm S. D. mg/kg)		Therian (range, mg/kg)	
Echidna	40 \pm 2.5	marsupials	40-300
Platypus	257 \pm 41	eutherians	65-200

The adrenal glands of both echidnas and platypus resemble those of other mammals in being paired, discrete organs adjacent to the kidneys and closely associated with chromaffin cells of the autonomic nervous system. However, structurally they are quite different. There is no arrangement of outer steroidogenic cells forming a cortex which surrounds the autonomic chromaffin cells. Instead, the steroidogenic cells form a large clump at one pole of the gland and the autonomic cells form a smaller one at the other pole (Fig. 1). At the microscopic level, too, the steroidogenic cells are not regularly arranged into cords with an outer glomerulosa, middle fasciculata and inner reticularis with distinct cell types. Instead, the cells are arranged in whorls and clusters without any regular pattern, and there are only two more or less distinct cell types, based on the amount of cytoplasm relative to nuclear material. Chester Jones (1957) considers the adrenal glands of the prototheria to resemble those of birds of reptiles in histological appearance.

In both species, the corticosteroids secreted by the steroidogenic cells are essentially similar to those found in most other vertebrates: those with known biological activity are cortisol, cortisone, corticosterone, and aldosterone. Analysis of adrenal venous blood has been made only in the echidna and in this species, as in birds and reptiles, the major corticosteroid was found to be the glucocorticoid

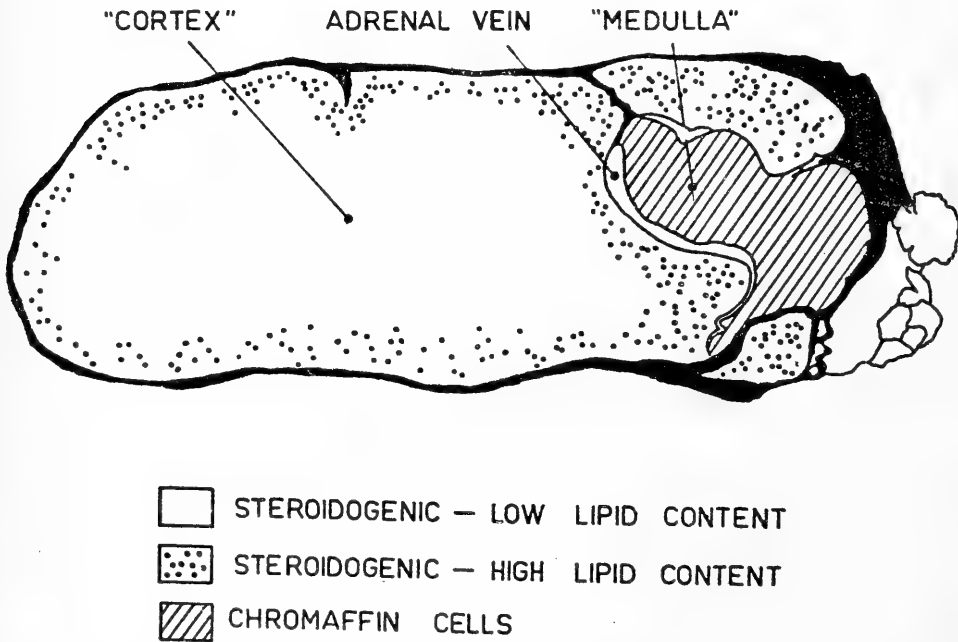


FIG. 1—Shadowgraph tracing of an adrenal gland from an adult echidna to show the relationship between steroidogenic ("cortical") and chromaffin ("medullary") cells.

MONOTREME ADRENOCORTICAL FUNCTION

corticosterone, although cortisol was also secreted at a much slower rate (Weiss and McDonald, 1965). Later measurements in conscious animals, using an indirect isotope dilution technique, indicate that the secretion rate of these two glucocorticoids are about equal, although corticosterone is still the major glucocorticoid in peripheral blood (Sernia and McDonald, 1977a; Table 2). The rate of this secretion, expressed either as a function of adrenal mass or body mass, is extremely low — being only about 1:100th that of most eutherians. On the other hand, the rate of secretion of the mineralocorticoid aldosterone (Table 2) is, relative to that of glucocorticoids, higher than in eutherians. Similarly, the concentration of the major corticosteroid in the peripheral blood plasma of the echidna is extremely low, being less than 0.1 ug 100 ml in the unstimulated state, compared with 1-20 in eutherian and metatherian mammals (Sernia and McDonald, 1977a).

TABLE 2

PLASMA CONCENTRATION AND SECRETION RATES OF MAJOR CORTICOSTEROIDS IN ECHIDNA (MEAN \pm S.D.) AND PLATYPUS (ONE ANIMAL ONLY).

Plasma concentration (ug/100 ml)		ECHIDNA	PLATYPUS
Cortisol		0.07 \pm 0.01	5.4
Corticosterone		0.14 \pm 0.04	1.8
Cortisone		Not Detected	8.2
Aldosterone (ng/100ml)		0.54 \pm 0.01	?
Secretion rate (ug/kg/hr)			
Cortisol (δ)		0.68 \pm 0.17	—
(ϕ)		0.43 \pm 0.29	—
Corticosterone (δ)		0.39 \pm 0.22	—
(ϕ)		0.29 \pm 0.16	—
Aldosterone (ng/kg/hr)		5.0 \pm 2.2	—

In contrast to the echidna the peripheral plasma total glucocorticoid concentration of the platypus is much higher (14-15 ug/100 ml) and well within the normal range of eutherian mammals. The platypus, however, is peculiar in that the major glucocorticoid is cortisone, in about twice the concentration of the other major glucocorticoid — corticosterone (Weiss, 1973). In eutherian mammals, the peripheral plasma concentration of cortisone is normally negligible. This much higher peripheral plasma concentration of glucocorticoids in the platypus supports the evidence from adrenal gland weight, that the adrenocortical secretions in the platypus may be much more significant in regulation of metabolism than in the echidna.

Adrenal homogenates of both species have been incubated *in vitro*, with and without radioactive glucocorticoid precursors; and both species appear to have enzyme systems for corticosteroid biosynthesis similar to those of other mammals, although some enzymes (particularly the 11 β and 17 α hydroxylase systems in the echidna) appear to be less active, relative to the enzyme systems earlier in the biosynthetic pathways (Weiss, 1973). Again, the platypus adrenal homogenates

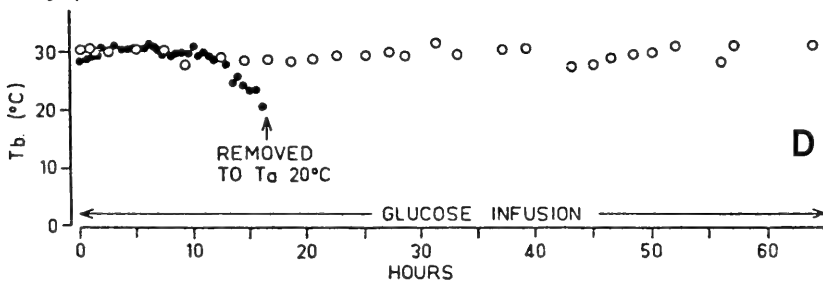
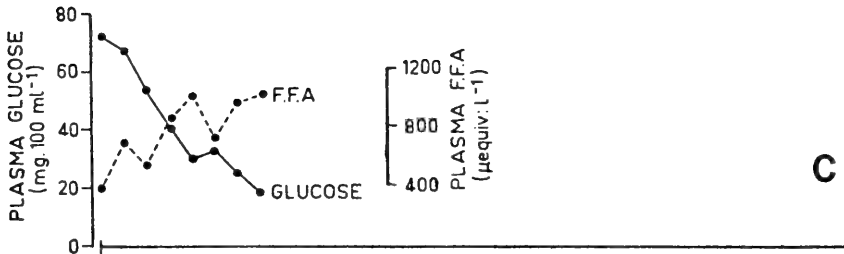
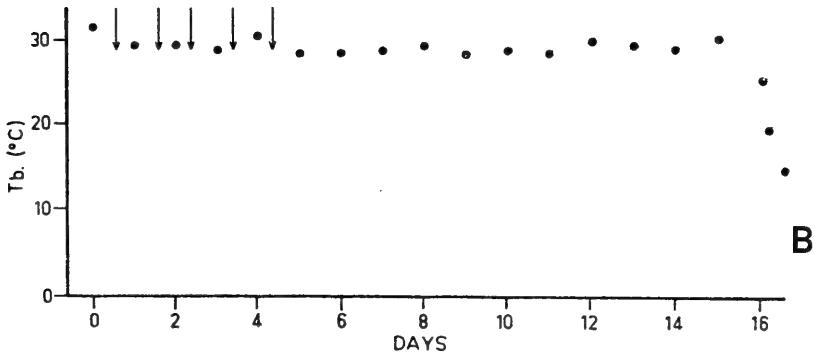
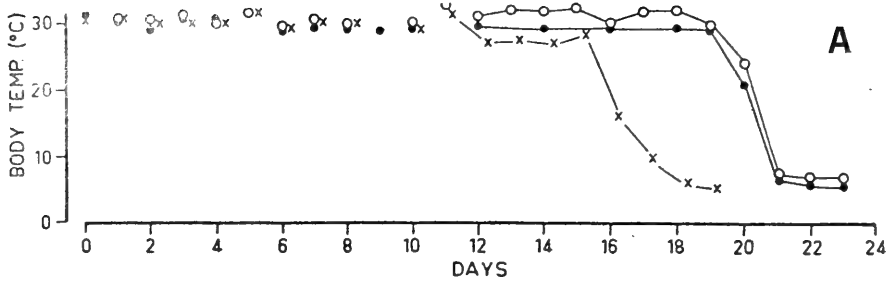


FIG. 2—Thermoregulation of echidnas exposed to ambient temperature 4°C from time 0. A. Body temperatures of three intact fasted echidnas. B. Body temperature of an adrenalectomised non-fasted echidna given 1 mg/gk cortisol acetate i.m. at times indicated by the arrows. C & D illustrate changes in FFA, glucose and body temp. of an untreated adrenalectomised echidna (closed circles). Body temp. of an adrenalectomised echidna treated with i.v. infusions of glucose (open circles) remains normal.

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produce a higher yield of corticosteroids from biosynthetic precursors than those from the echidna and the major *in vitro* product in the platypus homogenates is, again, cortisone. The adrenal homogenates of both species produce the mineralocorticoid aldosterone (Weiss, 1973) and its presence in adrenal venous blood of the echidna has been confirmed (Sernia and McDonald, unpublished).

We have no further information about adrenocortical functions in the platypus, and this is clearly a desirable topic to pursue. However, there have been extensive investigations into the control of adrenocortical secretions and the metabolic role of corticosteroids in the echidna.

EFFECT OF ADRENALECTOMY

The first and most obvious way to test the function of an endocrine gland is to remove it and see what happens. Echidnas tolerate bilateral adrenalectomy very well and can survive indefinitely with little evidence of abnormality, provided they eat, which they usually do (McDonald and Augee, 1968). If they do not eat, a single injection of a fairly large dose of the glucocorticoid, cortisol, will stimulate their appetite and they will again behave normally for periods measured in months (Augee, 1969). This seems to reinforce the idea, suggested by the small adrenal glands and low corticosteroid secretory activity, that adrenocortical secretions are not very important in metabolic regulations of echidnas. However, the longlasting effect of a single injection of cortisol suggests a minor role, and this has been tested in the following ways.

If adrenalectomised echidnas are exposed to an adverse environment (e.g. environmental temperature 4-10°C) it becomes apparent that they are in fact very different from normal. Intact echidnas, exposed to such a low environmental temperature, can increase their metabolic heat production and maintain normal body temperature indefinitely, provided they have access to adequate food. If they are fasted for about a week before exposure, their resistance fails, and usually after 1-2 weeks body temperature falls and they become torpid. Adrenalectomised echidnas, even though they may be provided with food *ad libitum*, cannot withstand such exposure to cold for more than 48 hours — usually only about 12 hours (Augee and McDonald, 1973). However, the adrenalectomised echidna can be made to behave like an intact echidna by injections of the glucocorticoid cortisol (Fig. 2B).

In intact, fasted echidnas and in adrenalectomised, non-fasted echidnas the fall in body temperature is always preceded by a drastic fall in plasma glucose concentration as shown for an adrenalectomised echidna in Fig. 2C, D (Augee and McDonald, 1972).

This leads naturally to the hypothesis that the fall in body temperature could be due to depletion of carbohydrate energy reserves. If one carries out the simplistic experiment of infusing glucose into an adrenalectomised echidna at the beginning of exposure to a low environmental temperature, to maintain the plasma glucose

concentration, it does, in fact, prevent the fall in body temperature which could otherwise occur (Fig. 2D). This suggests conformity with the classic idea of glucocorticoid action, as worked out for domesticated eutherian mammals; that glucocorticoids stimulate hepatic gluconeogenesis, mobilising tissue nitrogen for the purpose, so depositing glycogen in the liver and replenishing carbohydrate energy reserves, depleted by the metabolic response to a stressful environment.

The additional finding that fasted, intact, echidnas which have been exposed repeatedly to low environmental temperatures have markedly enlarged adrenal glands (about double the normal weight) reinforces the idea that the adrenal glands of echidnas do, in fact, respond in the same way as those of eutherian mammals to a stressful environment and are essential for an appropriate metabolic response (Augee and McDonald, 1973).

The natural range of adrenocortical steroid secretion rate and peripheral plasma concentration in conscious, unrestrained echidnas has recently been described (Sernia and McDonald, 1977a). If we examine in detail the actual metabolic actions of the naturally secreted corticosteroids, *within* the unstimulated and maximally ACTH stimulated levels of secretion, the picture is not as clear as it first seemed to be. Firstly, when cortisol or corticosterone are infused i.v. at rates corresponding to the maximally ACTH-stimulated secretion rate of 3 ug/kg/h (or even 10 times that rate) they cause, at the most, only a mild and irregular increase in plasma glucose concentration (Sernia and McDonald, 1977b). Very large doses of approximately 100 times the maximum ACTH-stimulated level do cause a significant increase (Augee and McDonald, 1973), indicating that the eutherian metabolic response is there, but not normally useable. Furthermore, treatment of echidnas by daily intramuscular injections of glucocorticoids, sufficient to raise their plasma glucocorticoid concentrations well above the ACTH-stimulated levels, have no effect on fasting liver glycogen concentration or on the urinary excretion of nitrogen (Sernia and McDonald, 1977b). So there is no evidence of nitrogen mobilisation nor of hepatic gluconeogenesis. Furthermore, these glucocorticoids do not affect the hypoglycaemic action of insulin (Sernia and McDonald, 1978).

What the glucocorticoids do do, however, is significantly increase plasma free fatty acid concentration (Sernia and McDonald, 1977b). This suggests that they may help mobilise energy reserves from fat depots. Augee (1969) found that the plasma free fatty acid concentration of intact echidnas, fasted and exposed to a low environmental temperature, was low at the time they failed to thermoregulate, whereas that of adrenalectomised echidnas was high. Also, in intact, non-fasted echidnas, infusion of ACTH causes a marked elevation of plasma free fatty acid which occurs much sooner than the increase due to glucocorticoid infusion (Sernia and McDonald, 1977b). This suggests that, as in other mammals, ACTH may have a direct fat-mobilising action.

From these observations it seems possible that the role of glucocorticoids secreted by the adrenal gland in response to stimulation by ACTH, when the

MONOTREME ADRENOCORTICAL FUNCTION

echidna is introduced into an adverse environment, is to synergise with ACTH in the mobilisation and utilisation of fat reserves to maintain the necessary increase in metabolic rate. The reason why plasma FFA is high in the adrenalectomised echidnas succumbing to a low environmental temperature could be that glucocorticoids are also essential for the cellular utilisation of the mobilised fat reserves.

On the basis of this hypothesis, the inability to utilise the mobilised fat reserves leads to consumption of the carbohydrate energy reserves in the form of liver glycogen. When this is depleted, plasma glucose concentration falls, leading to a drastic fall in metabolic heat production and thermoregulatory failure.

The fasted, intact echidna is already depleted of fat reserves, and so it is placed in the same position as the adrenalectomised echidna once these reserves are used up as a consequence of ACTH secretion in response to a cold environment. This would account for the low plasma FFA concentration at the time of hypoglycaemia and torpor in such animals. This is, so far, only an hypothesis, although the evidence in favour of it seems strong. This primary effect of glucocorticoids on fat, rather than carbohydrate and nitrogen metabolism, seems to be unique among the vertebrates so far examined, including birds and reptiles. However, strictly comparable experiments on these species have yet to be done.

It is clear therefore, that in spite of its extremely low level of secretory activity, the adrenal gland of the echidna must be essential for survival in a naturally stressful environment. It remains to be seen what the situation may be in the platypus, although the evidence so far suggests that it may be even more critical for survival in this species.

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Steroid-Binding Proteins in The Plasma of The Echidna, *Tachyglossus Aculeatus*, with Comparative Data for some Marsupials and Reptiles

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ABSTRACT

The binding of adrenocortical (cortisol, corticosterone) and gonadal (estradiol, dihydrotestosterone, testosterone) steroids by echidna plasma proteins was investigated by equilibrium dialysis and polyacrylamide gel electrophoresis. Some comparative data on 16 marsupial and 4 reptilian species are also included.

Purified echidna albumin behaved as a low-affinity, high capacity binding system with steroid affinity being inversely related to steroid polarity. In addition, a non-albumin high affinity, low capacity system was observed for E_2 and DHT; and a system of lower affinity and higher capacity for Te. A high affinity binding system for F and B analogous to eutherian CBG was not observed. Electrophoresis revealed distinct DHT- and E_2 -binding proteins with respective mobilities relative to albumin of 0.22 and 1.18; binding of B and F was absent.

The absence of a high affinity corticosteroid-binding protein, the presence of distinct DHT- and E_2 -binding proteins and the fast electrophoretic mobility of the E_2 binding protein, is in contrast to observations in both eutherian and metatherian mammals and in reptiles. However, the presence in the lizard *T. scincoides* of a minor E_2 -binding protein analogous to that of the echidna suggests that this protein may be found amongst reptiles.

INTRODUCTION

Plasma globulins exhibiting a high affinity for the major adrenocortical and gonadal steroids have been detected in all vertebrate classes (Seal and Doe, 1965; Idler, 1972). The biological inertness of steroids bound to these proteins (see Westphal, 1971; Anderson, 1974) suggests a physiological role in determining the metabolically active fraction of circulating steroids. The recent observation that a lowered concentration of corticosteroid-binding-globulin (CBG) is a factor leading to the post-mating mortality of male *Antechinus stuartii* (Bradley, McDonald and Lee, 1976; Bradley, 1977) clearly illustrates the physiological relevance of steroid-binding plasma proteins in non-eutherian mammals and highlights the need for similar studies where adrenocortical and reproductive endocrinology in marsupials

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or monotremes is to be assessed. This report deals with such an investigation in the echidna with the inclusion of some data on marsupial and reptilian species.

METHODS

Blood samples

Echidna blood was obtained either via a jugular catheter (Sernia and McDonald, 1977a) or by cardiac puncture. Blood from marsupials and reptiles was obtained by cardiac puncture. After separation of erythrocytes by centrifugation, the plasma was removed, treated with activated charcoal (50 mg/ml for 1h) to remove endogenous steroids, and stored at -20°C until required.

Equilibrium dialysis

0.5 ml samples of echidna plasma diluted 1:9 with 0.05M phosphosaline buffer, pH 7.4, were transferred to dialysis bags (8/32 Visking) and the bags closed by a tight knot. They were transferred to test tubes (1 x 7.2 cm) containing 2 ml of various concentrations of inert steroid buffer in addition to tracer amounts (4-6,000 DPM/ml) of radioactive steroid. Dialysis was performed in constant temperature room at 4°C or 30°C for periods of 36-48h which was sufficient time for equilibration. The concentration of bound and free steroid was calculated from the specific activity of the sac contents and the dialysate (Sandberg *et al*, 1966). The association constant (K) and concentration of binding sites ($[Z]_p$) were obtained from a Scatchard-type plot of the data (Scatchard, 1949).

Electrophoresis

Plasma proteins were separated electrophoretically in polyacrylamide gel by the method of Davis (1964); a spacer gel was omitted. Plasma (50 μ l) was incubated for 12h at 4°C with a tritiated steroid (70,000 DPM) and in some cases with 1-5 μ g of non-radioactive steroid. The sample was diluted with 50 μ l of 20% sucrose in Tris-HCl buffer (0.24 M, pH 6.7), layered on top of the gel rod, and electrophoresed at 4°C for 3-4h. The gel rod was then sliced with a razor-blade hand slicer (Matsumura and Noda, 1973) and the radioactivity measured after allowing each slice to stand in toluene scintillator for at least 4h.

Statistics

All data are expressed as mean \pm S.E.M. N denotes the number of animals.

RESULTS

EQUILIBRIUM DIALYSIS

Binding of cortisol (F) and corticosterone (B)

The ratio of bound: free for the binding of F and B to dilute (1:4) plasma at 4°C was 1.04 ± 0.08 (N = 7) respectively over a steroid concentration range of 0.6×10^{-8} M. The failure to saturate the binding sites (i.e. lower bound: free ratio) at such high steroid concentrations indicates a lack of high-affinity binding globulin in echidna plasma. However, low-affinity binding to the globulin fraction of plasma was present since the expected mean bound: free ratio for albumin, as calculated from the binding to a 1% solution of purified echidna albumin adjusted to the albumin concentration in each plasma sample (Doumas and Biggs, 1972), was only 0.66 ± 0.05 and 0.62 ± 0.08 for F and B respectively.

Figure 1 compares the distribution of F amongst plasma fractions in the echidna with that of the brush-tailed possum and man, which have a CBG. Unlike the echidna, the highest fraction of steroid is bound to globulin which becomes saturated as steroid concentration increases.

STEROID-BINDING IN ECHIDNA

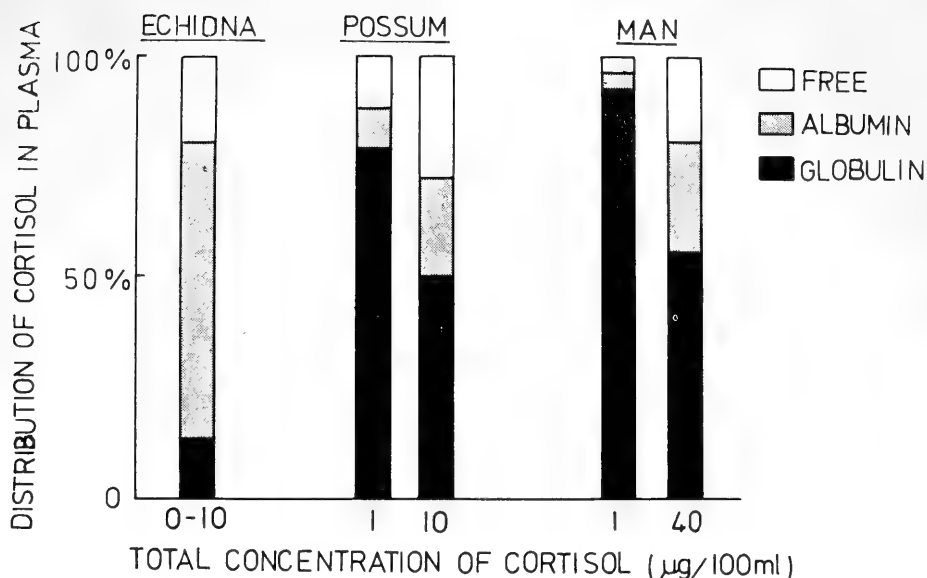


FIG. 1—Distribution of cortisol in the plasma of the echidna, brush-tailed possum and man. The absence of CBG in the echidna is evident from the low percentage of globulin-bound cortisol and the failure to saturate the binding sites. Data from Khin Aye Than and McDonald (1976) and Tait and Burstein (1964) were used to calculate distribution in possum and human plasma respectively.

Binding of 5 α -dihydrotestosterone (DHT), testosterone (Te) and 17 β -estradiol (E₂)

DHT, Te and E₂ were bound to a saturable globulin component of echidna plasma. The association constant was high for E₂ and DHT but much lower for Te (Table 1). The concentration of binding sites was lowest for E₂ and highest for Te. Binding to the albumin fraction, measured as the binding constant $K_A [\sum A]$ (Tait and Burstein, 1964), was in the following order of decreasing strength: E₂ > DHT > T.

Increasing the temperature from 4° to 30°C decreased the association constants by 50-64% and the albumin binding constants by 32-38%.

Specificity

The ligand specificity of the binding protein(s) was examined by measuring the competitive displacement of a radioactive tracer of one of the three gonadal steroids by a second non-radioactive steroid. Table 2 shows that the bound: free ratio of Te, DHT and E₂ decreased in the presence of a second non-radioactive steroid. However Te and E₂ were displaced to a lesser extent than DHT, even at the high concentrations of steroids used for this experiment.

ECHIDNA

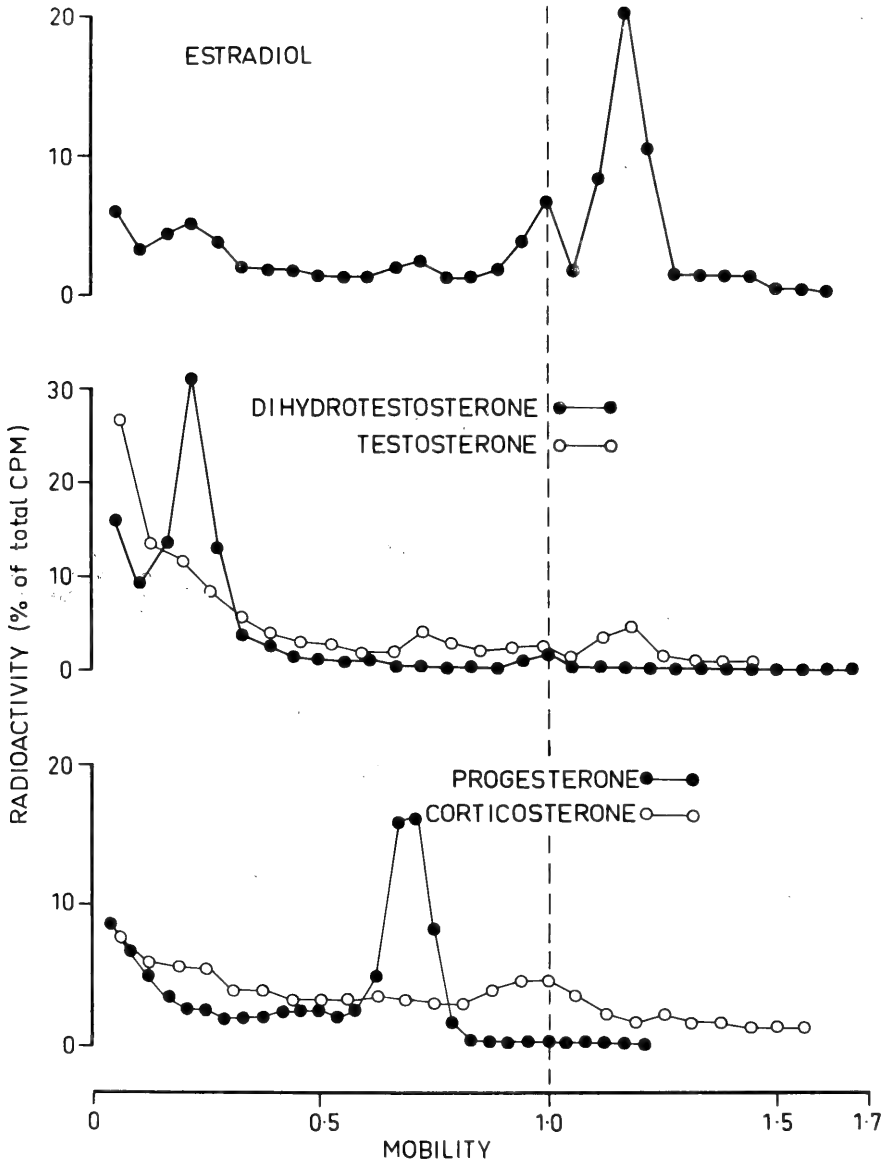


FIG. 2—Polyacrylamide gel electrophoresis of echidna plasma showing separate binding proteins for estradiol, dihydrotestosterone and progesterone but not for testosterone and corticosterone. The horizontal axis represents mobility relative to albumin.

STEROID-BINDING IN ECHIDNA

TABLE 1

ASSOCIATION CONSTANTS AND BINDING CAPACITIES FOR SEX STEROIDS IN ECHIDNA PLASMA

Steroid	No. of	Temp. °C	Association Constant l/mol	Binding Capacity mol/l	Albumin Binding Constant (a)
E ₂	8(4M, 4F)	4	$2.32 \pm 0.59 \times 10^9$	$5.90 \pm 1.36 \times 10^{-8}$	46.94 ± 3.08
	8(4M, 4F)	30	$8.41 \pm 2.13 \times 10^8$	$5.98 \pm 1.24 \times 10^{-8}$	30.30 ± 1.98
DHT	7(4M, 3F)	4	$3.44 \pm 0.48 \times 10^8$	$1.50 \pm 0.11 \times 10^{-7}$	28.78 ± 1.88
	8(5M, 3F)	30	$1.73 \pm 0.30 \times 10^8$	$1.28 \pm 1.28 \times 10^{-7}$	19.53 ± 1.28
Te	10(6M, 4F)	4	$4.26 \pm 1.11 \times 10^6$	$1.27 \pm 0.32 \times 10^{-5}$	19.36 ± 1.10
	8(4M, 4F)	30	$2.05 \pm 0.49 \times 10^6$	$1.05 \pm 0.15 \times 10^{-5}$	12.03 ± 0.76

(a) Calculated as the product of the mean concentration of albumin in the plasma of 7 male and 6 female echidnas (4.20 ± 0.30 g/100 ml) and the bound : free ratio for each steroid in a 1% solution of purified echidna albumin.

ELECTROPHORESIS

The large difference in the concentration of binding sites for each of the three gonadal steroids (Table 1) and the lack of competitive displacement of E₂ or Te (Table 2) indicates the presence of more than one sex-hormone-binding globulin (SHBG). This possibility was examined by electrophoretic characterisation of the binding proteins (Figure 2).

The lack of a high-affinity protein for B confirmed the results obtained by dialysis (previous section). However, progesterone, which is bound by CBG in eutherian mammals, was bound by a protein with a mobility like that of human CBG in this electrophoretic system.

Two distinct SHBG systems were present; one with a high relative mobility (1.18) and a high specificity for E₂ (E₂-SHBG) and a second with a low mobility (0.22) and a high specificity for DHT (DHT-SHBG). Only minor binding of Te, of dubious significance, was present.

Binding proteins in marsupials

The co-existence of two SHBG systems has not been observed in eutherian mammals which have a single SHBG with a mobility like echidna DHT-SHBG that binds both androgens and estrogens. The possibility that marsupials also possess a non-eutherian pattern was examined by a survey of 16 species from 7 marsupial families (Figure 3, Table 3).

A CBG-like protein with a high affinity for both cortisol and progesterone and a relative mobility of 0.58-0.77 was found in all 16 marsupials. The red kangaroo, quokka, koala and bandicoot also showed a second CBG with a lower relative

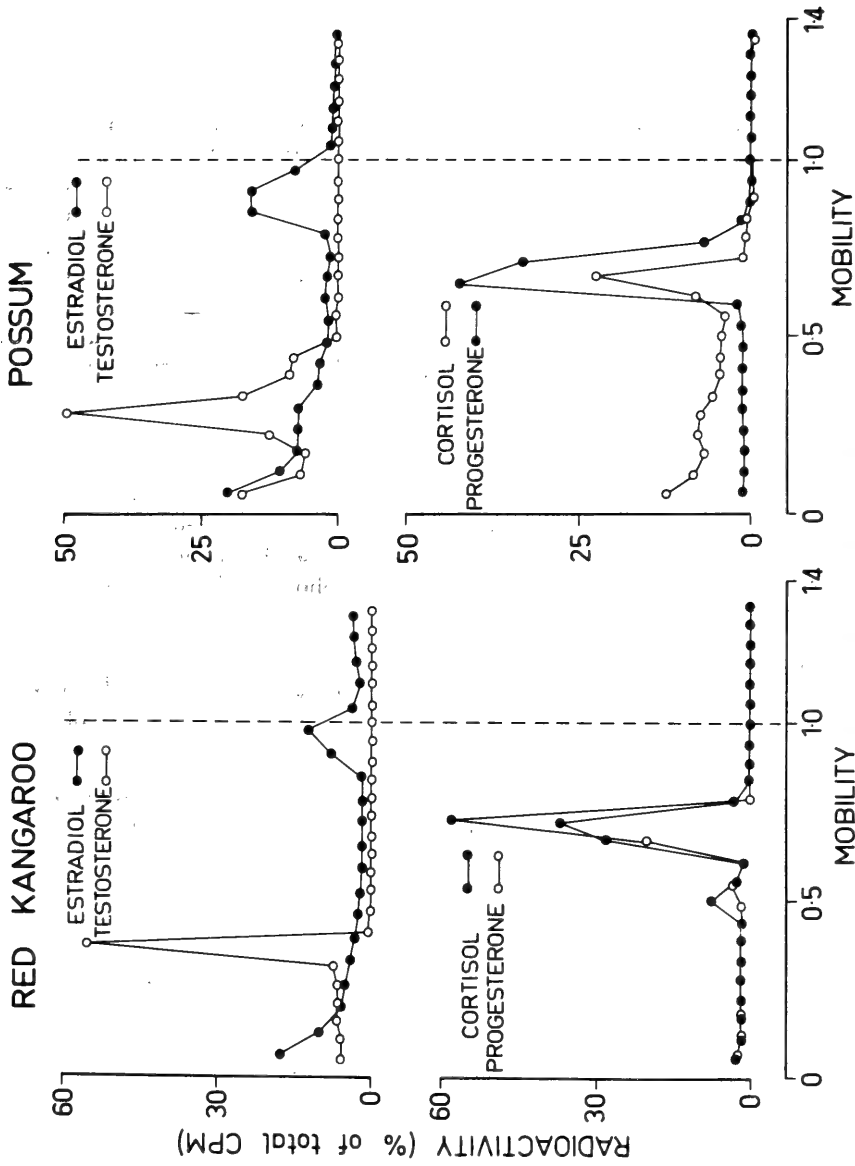


FIG. 3—Steroid-binding proteins in the plasma of a macropodid (*M. rufus*) and a phalangerid (*T. vulpecula*) marsupial. The mobilities of the two proteins are similar to the eutherian counterparts but marsupial SHBG does not bind estradiol.

STEROID-BINDING IN ECHIDNA

mobility of 0.50-0.56. In addition, a SHBG-like protein with a relative mobility of 0.28-0.43 was found in 7 species which, unlike eutherian SHBG, bound testosterone but not estradiol.

Binding proteins in reptiles

The E₂-SHBG of the echidna may be a legacy from its reptilian ancestry retained also by some modern reptiles. It was therefore of interest to characterise steroid-binding proteins in reptiles. Two snakes (*N. scutatus* and *P. textilis*), a tortoise (*C. longicollis*) and a lizard (*T. scincoides*) were examined (Figure 4).

Separate CBG and SHBG molecules were not observed; instead, a single major protein bound both adrenocortical and gonadal steroids. It is highly likely that these steroids share a single type of binding site since tritiated testosterone or cortisol bound to tiger-snake plasma was easily displaced by both non-radioactive testosterone and cortisol (Figure 5). The two elapid snakes *Notechis scutatus* and *Pseudonaja textilis* showed a second very minor binding protein of low mobility as well as binding of E₂ to albumin. The blue-tongued lizard, *Tiliqua scincoides*, clearly showed a minor E₂-specific protein in the pre-albumin region, similar to the echidna E₂-SHBG.

DISCUSSION

High-affinity binding of the major glucocorticosteroids to plasma proteins has been found in all terrestrial vertebrate species so far examined, including marsupials

TABLE 2
COMPETITIVE DISPLACEMENT OF RADIOLIGANDS IN ECHIDNA PLASMA.

Inert Steroid	Radioligand		
	Te	DHT	E ₂
NONE			
bound : free	6.9	18.5	18.5
Te			
bound : free		4.1 (78%)	15.5 (16%)
concentration		1.5 x 10 ⁻⁵ M	2.6 x 10 ⁻⁵ M
DHT			
bound : free	4.7 (32%)		16.0 (14%)
concentration	5.8 (16%)		5 x 10 ⁻⁶ M
E ₂			
bound : free	3.8 x 10 ⁻⁶ M	7.7 (58%)	
concentration	4.2 x 10 ⁻⁶ M	5 10 ⁻⁶ M	

Plasma was diluted 1 : 9. Numbers in parenthesis represent % displacement.

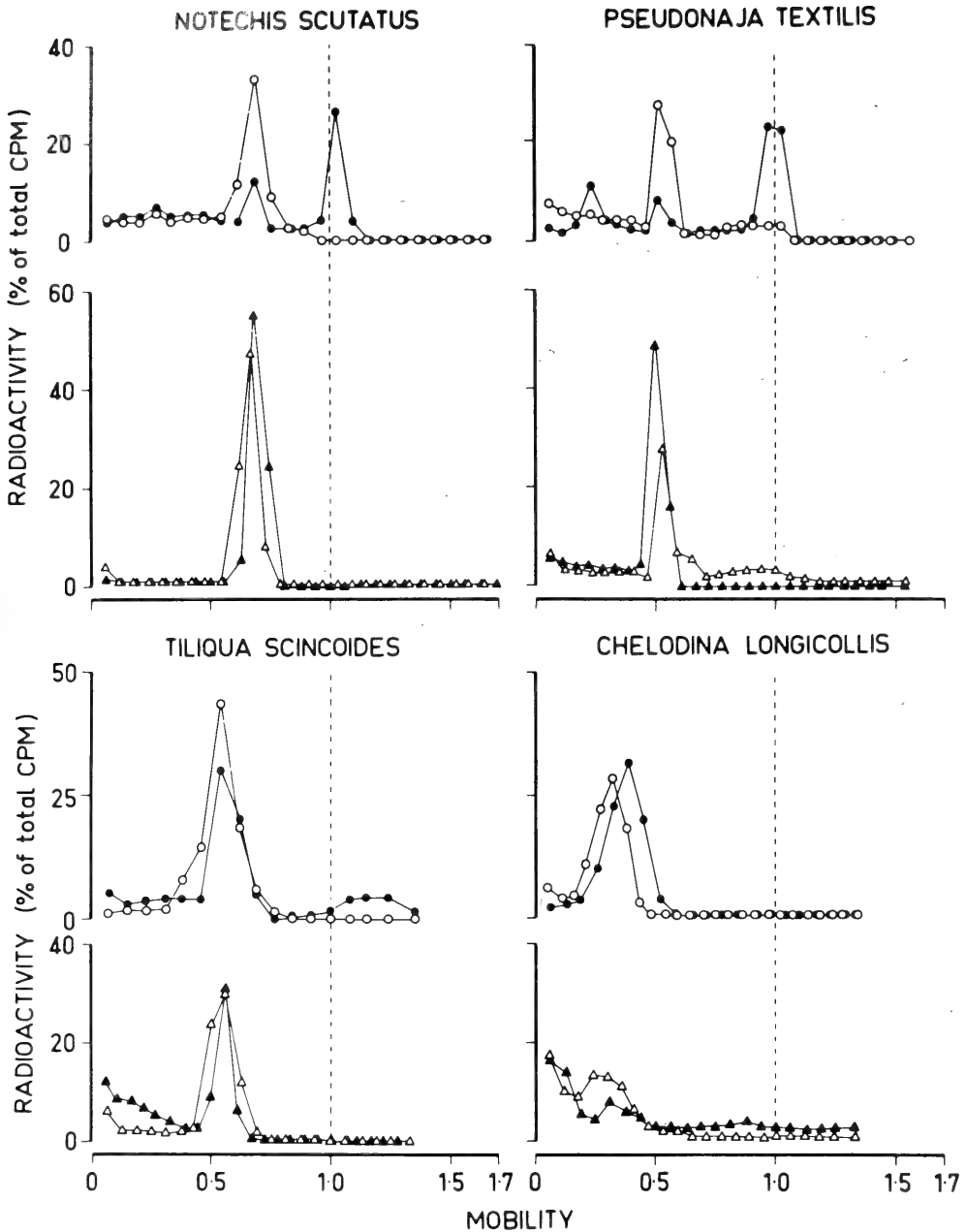


FIG. 4—Steroid-binding proteins in the plasma of reptiles. Estradiol (●), testosterone (○), cortisol (▲) and progesterone (△) are bound to a single major protein in all four species. *T. scincoides* shows an additional minor estradiol-specific protein in the pre-albumin region.

STERIOD-BINDING IN ECHIDNA

(Seal and Doe, 1965; Khin Aye Than and McDonald, 1976; Bradley *et al*, 1976; Cook, Sutterling, Graber and Nalbandov, 1977; Bradshaw and McDonald, 1977). However in this investigation, both equilibrium dialysis and polyacrylamide gel electrophoresis of echidna plasma failed to show the presence of an analogous binding system.

When viewed in terms of the low adrenocortical activity of conscious, unstressed echidnas (see McDonald, this Volume) — especially the plasma glucocorticosteroid concentrations of only 1-3 ng/ml and the capacity to survive adrenalectomy indefinitely (McDonald and Augee, 1968, Sernia and McDonald, 1977a), this exceptional absence of corticosteroid-binding provides further confirmation of the minimal role of adrenal steroids in the metabolism of echidnas in conditions of low stress. However, an adequate adrenocortical response is essential during long-term stress (Augee and McDonald, 1973) and in this case the lack of CBG may be seen to have a survival value since the already low secretory capacity of the adrenal cortex would not be further limited by the maintenance of a biologically inert pool of circulating glucocorticosteroids. On the basis of these considerations, it may in fact be argued that, because of its association with a lack of CBG and the limited need for glucocorticosteroids to extreme conditions (stress), the low secretory capacity of the echidna adrenal cortex does not represent an ancestral mammalian trait but the evolution to a stage of maximal efficiency.

TABLE 3

HIGH AFFINITY STEROID BINDING IN MARSUPIAL PLASMA

Family	Species	Steroid Tested			
		Cortisol	Progesterone	Testosterone	Estradiol
Macropodidae	<i>M. rufus</i>	+	+	+	—
	<i>S. brachyurus</i>	+	+	—	—
	<i>T. billardieri</i>	+	+	+	+
	<i>W. bicolor</i>	+	+	+	—
	<i>M. giganteus</i>	+	+	+	—
	<i>M. eugenii</i>	+	+	—	—
	<i>M. rufogriseus</i>	+	+	+	—
	<i>P. tridactylus</i>	+	+	—	—
Phalangeridae	<i>T. vulpecula</i>	+	+	+	—
Petauridae	<i>P. peregrinus</i>	+	+	—	—
Peramelidae	<i>I. macrourus</i>	+	+	+	—
Vombatidae	<i>V. ursinus</i>	+	+	—	—
Phascolarctidae	<i>P. cinereus</i>	+	+	+	—
Dasyuridae	<i>A. stuartii</i>	+	+	—	—
	<i>S. harrisi</i>	+	+	—	—
	<i>S. crassicaudata</i>	+	+	—	—

+ Denotes presence and — absence of binding as detected by polyacrylamide gel electrophoresis.

NOTECHIS SCUTATUS

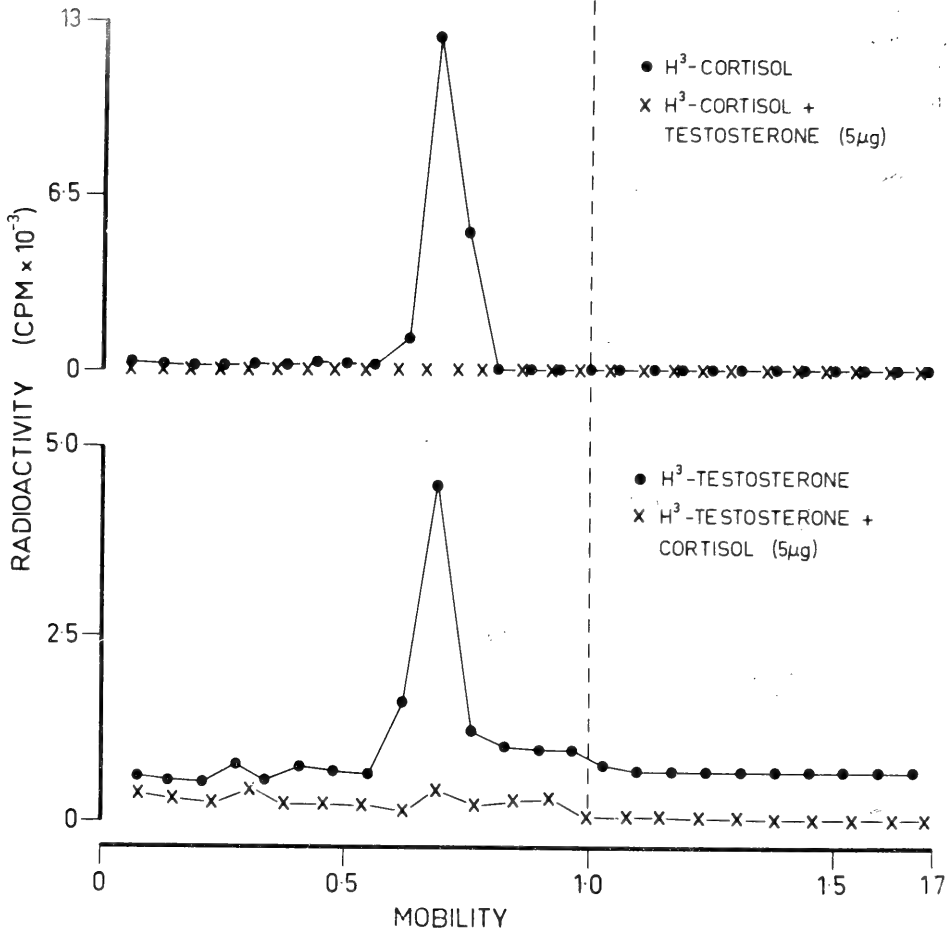


FIG. 5—Displacement of 3H -cortisol by testosterone and of 3H -testosterone by cortisol in the plasma of the tiger snake, suggesting that both steroids share a common set of binding sites.

The binding of progesterone to a protein with a mobility like eutherian CBG suggests that the echidna once possessed CBG but, as a consequence of the low adrenocortical activity, the specificity for the corticosteroids was lost. An investigation of the platypus, which has a high adrenocortical activity, should elucidate this point.

The E_2 -SHBG in echidna plasma is unlike eutherian SHBG which migrates as a β -globulin (Rosenbaum, Christy and Kelly, 1966). However, the E_2 -binding

STEROID-BINDING IN ECHIDNA

to a broad band of pre-albumin proteins in the plasma of the blue-tonged lizard (*T. scincoides*; Figure 4) indicates that a similar 'fast' E₂-SHBG may be present amongst reptiles. Because of its phylogenetic significance, this aspect is worth extending to other reptiles and the platypus. The four reptiles in this investigation are the only reptilian species where E₂-binding to plasma proteins have been studied to date. The unusual binding characteristics of reptilian steroid-binding proteins also promise to be of interest in themselves and may have a bearing on the high concentrations of adrenal and gonadal steroids often observed in reptiles.

Echidna E₂-SHBG and eutherian SHBG also differ in their relative affinities for E₂, DHT and T with echidna E₂-SHBG having relative affinities for E₂ >> DHT = T, while eutherian SHBG shows relative affinities for DHT > T > E₂. On the other hand there are striking similarities between echidna DHT-SHBG and eutherian SHBG; both have low electrophoretic mobilities and both have relative affinities for DHT > T > E₂, but whereas eutherian SHBG has a high affinity for all three, echidna DHT-SHBG binds E₂ very weakly. This dichotomy between androgen and estrogen specificity is even more obvious in the marsupials where E₂-binding was absent from all species investigated.

The basic similarities of the low-mobility SHBG from all three mammalian groups suggests a common evolutionary origin with the differences in the relative affinities for DHT, T and E₂ being a product of divergence in reproductive function. In this context, it may also be postulated that the echidna retained a "fast" E₂-SHBG along with a reptile-like mode of reproduction while the therian mammals lost this protein as a consequence of their divergence from reptilian reproduction. The invariable presence of "SHBG" in the reptiles included here and those in the report by Corvol and Bardin (1973), in contrast to the complete loss of SHBG in many metatherian and eutherian species, supports this hypothesis. However, it is important to note that, apart from the possible existence of a "fast" SHBG in some reptiles, the electrophoretic and steroid-binding properties of binding proteins in the echidna are vastly different from those of modern reptiles.

ACKNOWLEDGEMENTS

Mr Ron Waters and Professor A. K. Lee of the Department of Zoology, Monash University, and Mr John Seebeck of the Arthur Rylah Institute are gratefully acknowledged for samples of blood from reptiles and marsupials. Part of this investigation was performed under the supervision of Dr. I. R. McDonald, Monash University, and submitted for the Ph.D. degree.

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Metabolism and Temperature Regulation in the New Guinea Monotreme *Zaglossus Bruijni*

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The monotremes are the only extant representatives of the earliest radiation of mammals, the prototherians, and so are centrally important to any discussion about the evolution of mammalian homeothermy with its high stable body temperatures. While they are obviously highly specialised, monotremes may still retain characters that will give us insight into the physiology of early mammals. The thermoregulatory and metabolic capabilities of the echidna *Tachyglossus aculeatus* and the platypus *Ornithorhynchus anatinus* have been examined in several studies since the early work of Martin in 1902; the interpretation of the results of these studies have varied considerably however. *Zaglossus bruijni* belongs to the third extant genus of monotremes and information about its thermoregulatory characteristics is limited to a few observations on body temperature (Dawson, 1973a). These measurements indicated that *Z. bruijni* has a monotreme-like body temperature of approximately 30°C.

We were able to examine two *Z. bruijni* through the kind co-operation of Taronga Zoological Park, Sydney. The animals had come from the highlands of New Guinea and were kept in the Zoo's nocturnal house. The mean weights of the animals during the study were 10.7 kg and 16.53 kg. Sex could not be determined. Oxygen consumption (heat production) and total evaporative water loss were estimated using an open circuit technique. The *Z. bruijni* were fasted for 24h and then placed in a strong wire cage inside a 0.3 by 0.3 by 0.5 m perspex chamber with an airtight lid. Inlet and outlet connections were placed at opposite ends of the chamber. Dry air flowed through the chamber at a constant rate. Flows between 3 and 6 l/min were selected and measured with a calibrated dry gas meter. The chamber was placed in a controlled temperature box which could be controlled to $\pm 0.5^{\circ}\text{C}$. Temperatures were measured with copper-constantan thermocouples and a Leeds and Northrup Speedomax W recording potentiometer. Body temperature was measured as deep colonic temperature. The equipment and techniques used were essentially similar to those used in other studies from this laboratory, such as Dawson (1973b).

Heat production was calculated assuming a respiratory quotient of 0.8 and 1 ml O₂ g⁻¹ h⁻¹ equated with 5.59 W kg⁻¹. Conductance was calculated using the equation of Dawson and Schmidt-Nielsen (1966); for this a Meeh factor of 9.0 was assumed for surface area estimation. The animals were allowed to come into equilibrium at each air temperature, and measurements were only made when oxygen consumption and body temperature were stable; this generally took from 2-3 hours.

The results shown in Figure 1 indicate that metabolic rate and body temperature are lowest at 20°C but are only slightly elevated at air temperatures down to 15°C and up to 30°C. This is expected for such large animals. The most noticeable point is that while the body temperature was similar to those reported previously for other monotremes (Dawson, 1973a) the metabolic rate was much lower. The mean minimum oxygen consumptions of the two animals were 0.087 and 0.075 ml g⁻¹ h⁻¹ for the small and large animals respectively. These values are approximately a quarter of the values which would be predicted for eutherians from the work of Kleiber (1961).

The pattern of heat loss was interesting (Figure 2). Heat loss, as indicated by conductance, was low at a T_{air} of 15°C and in fact the mean conductance at this temperature (0.58 W m⁻² °C⁻¹) was only half that observed in the platypus at low air temperatures (Grant and Dawson, 1978). The relatively large body size with its low surface area to body weight ratio and the dense long fur would contribute to this difference (fur length was approximately 23mm on the dorsal surface). Conductance rapidly increased above a T_{air} of 20°C, suggesting a considerable increase in peripheral blood flow to facilitate heat dissipation. Evaporative heat loss was also elevated at the higher air temperatures examined. At a T_{air} of 30°C evaporation accounted for approximately 73% of the total heat lost. It should be remembered that there was a relatively small amount of heat to be lost, but it seems unlikely that an increased respiratory evaporation accounted for the higher evaporation. At the highest temperature respiratory rate actually fell, and if the pattern in *Z. bruijini* is comparable to that shown by Augee (1976) for *T. aculeatus*, then respiratory ventilation would also fall. A possible answer is an increased passive diffusion of water through the skin associated with an increased peripheral blood flow. Another answer however is sweating. *Tachyglossus aculeatus* does not sweat and does not possess significant numbers of sweat glands, but this may not be the case for *Z. bruijini*. Griffiths (1968) cites a report that *Z. bruijini*, unlike *T. aculeatus*, has well developed apocrine sweat glands all over its dorsal and ventral surfaces. One of our animals struggled for a short while at a T_{air} of 30°C and body temperature was elevated to 34.8°C. When the animal was removed from the chamber it was covered with what seemed to be sweat. Consideration for these valuable animals, and their keepers, precluded our further investigations into sweating, but sweating is possibly the explanation for the elevated evaporative heat loss. The platypus also sweats (Augee, 1976; Grant and Dawson, 1978).

ZAGLOSSUS TEMPERATURE REGULATION

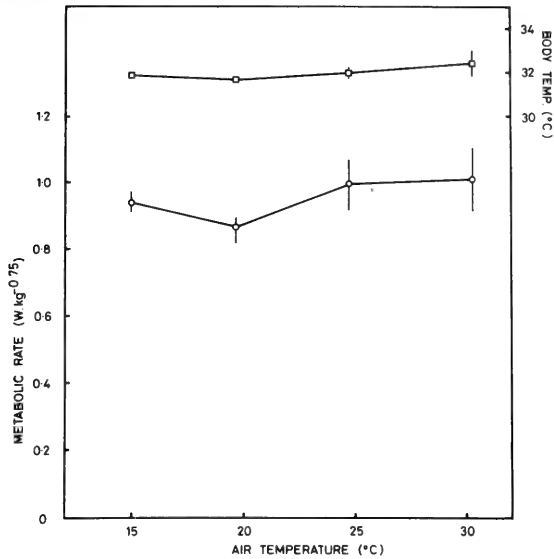


FIG. 1.—Body temperature (□) and heat production (O) of *Zaglossus bruijni* in equilibrium at various air temperatures. Values are the mean result for the two animals; vertical bars indicate the range of values obtained in individual experiments.

The very low metabolic rates which we obtained puzzled us somewhat, particularly so because recent data from this laboratory (Grant and Dawson, 1978) has indicated a relatively high metabolic rate for the platypus. This prompted us to also re-examine *Tachyglossus aculeatus* using the same equipment and procedures and look in detail at platypus metabolic rates (Dawson, Grant and Fanning, 1979). These results are summarised in Table 1 (together with information on marsupials and eutherians). The value for the standard metabolic rate (SMR) of *T. aculeatus* is only marginally higher than that of *Z. bruijni* on a weight independent basis. These data are generally much lower than the minimal values reported by Schmidt-Nielsen et al (1966). Augee (personal communication) has provided us with the weights and values for the individual animals in his recent study on *T. aculeatus* (Augee, 1976) and recalculation of this information shows that his mean minimal metabolic rates for *T. aculeatus* are of the same order as our data, approximately $1.2 \text{ W kg}^{-0.75}$. A. J. Hulbert (personal communication) has also informed us that he has obtained minimal rates for *T. aculeatus* similar to those we obtained. It now appears that although the two members of the Family Tachyglossidae, have differing SMR's they do, as might be expected, form a group which is metabolically distinct from *Ornithorhynchus anatinus*.

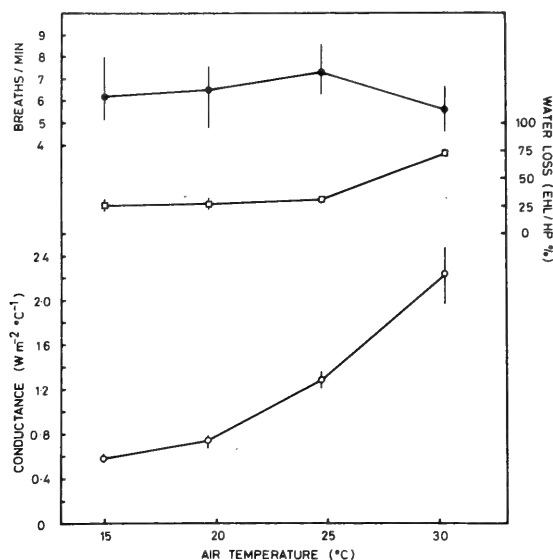


FIG. 2—Variation of conductance (O), the proportion of metabolic heat lost by evaporation (□), and respiration rate (●) with air temperature in *Zaglossus bruijnii*. Values are the mean result for the two animals; vertical bars indicate the range of values obtained in individual experiments.

TABLE 1

STANDARD METABOLISM AND BODY TEMPERATURES¹ OF MONOTREMES AND OTHER MAJOR MAMMALIAN GROUPS².

Animals	Weight range kg	T _{body} °C	Heat production W kg ^{-0.75}
<i>Zaglossus bruijnii</i>	10.7 — 16.5	31.7 ± 0.07	0.86 ± 0.02
<i>Tachyglossus aculeatus</i>	2.6 — 4.2	31.3 ± 0.62	0.98 ± 0.05
<i>Ornithorhynchus anatinus</i>	1.0 — 1.6	32.1 ± 0.16	2.21 ± 0.22
Marsupials	—	35—36	2.35
Eutherians	—	38	3.34

1. Measurements made in thermoneutrality.

2. Data from Dawson, Grant and Fanning (1979).

ZAGLOSSUS TEMPERATURE REGULATION

It is not possible to draw any significant evolutionary conclusions from this information, largely because of paucity of the fossil history of the monotremes. As discussed in this symposium (Archer et al., 1978) the only Tertiary monotreme fossil *Obdurodon insignis* from the Miocene of South Australia (Woodburne and Tedford, 1975) is referable to the Ornithorhynchidae. Thus the platypuses have been a distinct line for a long time. The evolutionary acquisition of an elevated metabolism is a common feature in many aquatic and semi-aquatic mammals, this elevation being presumably related to their thermally demanding environment (Irving, 1973). It is possibly aquatic habitation which has led to the difference in metabolic rates between the two monotreme families, rather than some generalised phylogenetic change such as seen between marsupials and eutherians (Dawson and Hulbert, 1970).

ACKNOWLEDGEMENTS

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Metabolic Consequences of Subspecific Pelage Variations in the Echidna

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ABSTRACT

The distribution of *Tachyglossus aculeatus* on mainland Australia and Tasmania is clinal in relation to pelage. The Northern subspecies *acanthion* has much less fur than the Tasmanian subspecies *setosus*, and upon exposure to cold *acanthion* has a lower mean body temperature and a higher mean oxygen consumption than *setosus*. Values for the subspecies *aculeatus* captured in Victoria are intermediate. Metabolic differences between the subspecies are removed by acclimation.

INTRODUCTION

The genus *Tachyglossus* is generally considered to have but one species, *aculeatus* (Griffiths 1968). The species distribution on mainland Australia and Tasmania is clinal in relation to pelage, with the Northern forms being less hairy than the Tasmanian forms. This is well illustrated by the three subspecies used in this study:

- T. a. acanthion* hair or bristles on dorsal surface very short and scarce; spines long and stout. Animals captured in central Queensland.
- T. a. aculeatus* hair is sparse on ventral surface, but covers entire body. Spines obscure hair on dorsal surface. Animals captured in Eastern Victoria.
- T. a. setosus* pelage soft, thick and woolly. Spines fewer than other subspecies and obscured by pelage. Subspecies restricted to Tasmania.

Echidnas of the subspecies *T. a. aculeatus* are heterothermic, and although they are capable of greatly increased metabolism in response to low ambient temperatures (Augee 1976) their body temperatures decrease with inactivity even under natural winter conditions (Augee *et al.*, 1970). Various studies have been undertaken to examine the capabilities and control of heat production in echidnas, but little attention has been paid to the equally important question of heat loss and its control. Since the above subspecies have obvious differences in insulation, they

are used in the present study to examine the role of heat loss in temperature regulation of echidnas.

MATERIALS AND METHODS

The experimental group comprised seven *T. a. aculeatus*, five *T. a. setosus* and three *T. a. acanthion*.

Body temperatures (T_b) were taken once in the morning, once in the afternoon and once in the evening by means of a thermocouple probe inserted through the base of a spine as previously described (Augee and Ealey 1968). Oxygen consumption was determined using open circuit respirometry and a Kipp and Zonen Diaferometer (MG4).

The experiments were carried out from Aug. to Nov. in a constant temperature room capable of holding the designated temperature within 0.5°C . In order to study acclimation, the animals were held at least a week at each level of ambient temperature (T_a), and the T_a was lowered to 5°C and then raised to 30°C in a stepwise manner as shown:

T_a	
20°C	16 days
15	7
10	14
5	21
10	7
15	7
20	7
25	7
30	7

Food as described by Augee and Ealey (1968) was supplied *ad lib* throughout the study. All animals retained normal body weight, and there were no instances of torpor.

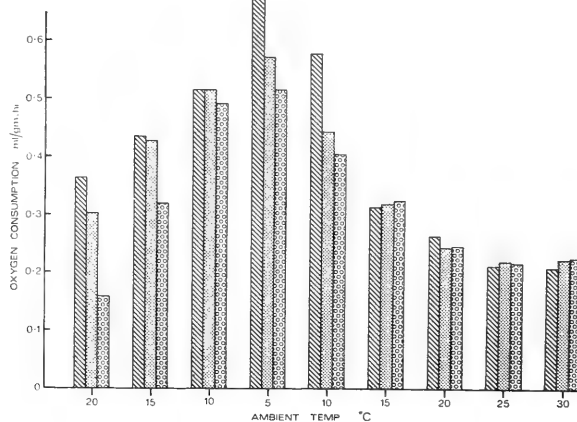
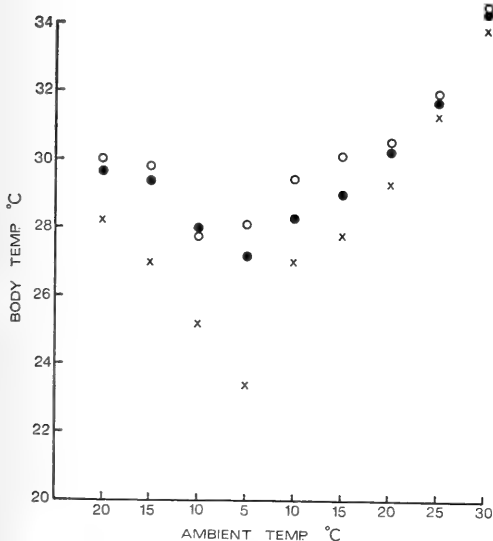


FIG. 1.—Mean T_b for animals of the subspecies *Tachyglossus aculeatus setosus* (open circles), *T. a. aculeatus* (closed circles) and *T. a. acanthion* (crosses) upon exposure to T_a regimes as described in text.

FIG. 2.—Mean oxygen consumption for animals of the subspecies *Tachyglossus aculeatus acanthion* (diagonal stripes), *T. a. aculeatus* (solid dots) and *T. a. setosus* (open circles) upon exposure to T_a regimes as described in text.

ECHIDNA PELAGE VARIATIONS

RESULTS AND DISCUSSION

From the beginning of the study when animals were held at T_a 20°C, the three subspecies differed in T_b (Fig. 1) and oxygen consumption (Fig. 2). Predictably, on the basis that the sparser the pelage the greater the heat loss, T_b of the subspecies *acanthion* was lower and its oxygen consumption greater than the other two subspecies. T_b was highest and oxygen consumption lowest for the Tasmanian subspecies *setosus*. The difference between the two extremes was exaggerated as T_a was lowered to 5°C. However as T_a was raised, the values for all three subspecies came closer together. This can clearly be seen by comparing the oxygen consumption values obtained at initial exposure to T_a 20 and 15°C with those obtained upon the second exposure. The effect of acclimation was not only to decrease the subspecific differences but also to increase mean T_b and decrease mean oxygen consumption in the two subspecies with the least fur (*acanthion* and *aculeatus*). This acclimation effect is further illustrated by changes in conductance.

Conductance is the biological expression of Newton's law that heat loss from a body is proportional to the surface area of that body and the heat differential between it and the environment. In biological systems it is easier to measure heat production (HP, usually as oxygen consumption), and conductance is often expressed as cal per unit surface area (cm^2) per hour per °C temperature differential ($T_b - T_a$). A plot of heat production (as oxygen consumption) vs. temperature differential for each of the three subspecies on their FIRST exposure to T_a decreasing from 20 to 5°C is shown in Fig. 3. According to Newton's law of cooling, when $HP=0$, $T_b=0$. Therefore I have drawn the line of best fit for each subspecies to pass through the origin. The slope of each line, designated 'C' in Table 1, is expressed in ml O_2 per gram body weight per hour per °C temperature difference. To convert ml O_2 consumed to cal produced, I have assumed that 1 ml O_2 represents 4.7 cal of heat produced. In order to make comparisons between the subspecies and with published data on the basis of surface area, I have calculated

TABLE 1

CONDUCTANCE VALUES FOR SUBSPECIES OF *TACHYGLOSSUS ACULEATUS*
DERIVED FROM FIG. 3.

	ml O_2 /gm/hr/°C	cal/cm ² /hr/°C
<i>T. a. acanthion</i>	0.037	0.336
<i>T. a. aculeatus</i>	0.028	0.254
<i>T. a. setosus</i>	0.022	0.195
<i>T. a. aculeatus</i> from Schmidt-Nielsen <i>et al</i> (1966)	—	0.15

"C" is derived as explained in the text.

surface area (S) from the equation $S=10 W^{0.67}$. Neither assumption has been verified for monotremes. To reach the final expression for comparison of conductance ($\text{cal}/\text{cm}^2/\text{hr}/^\circ\text{C}$) I have used the slope 'C' for each subspecies adjusted to a 'mean' echidna weighing 4 kg (and therefore having a surface area 2072 cm^2). Table 1 compares this calculated conductance for each subspecies with the only value in the literature (Schmidt-Nielsen *et al*, 1966). Conductance for the least hairy subspecies, *acanthion*, is 1.7 times greater than that for the hairiest subspecies, *setosus*. This represents a greater rate of heat loss in the former subspecies. The value for *setosus* is in reasonable agreement with the published value.

A plot of oxygen consumption vs. temperature differential for the three subspecies upon their SECOND exposure to T_a 10, 15 and 20°C is shown in Fig. 4. Except for the initial (T_a 10°C) value for *acanthion*, there is no significant

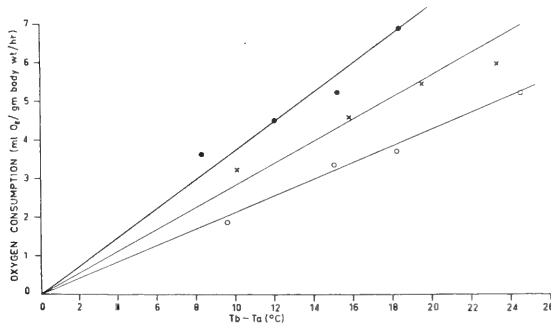


FIG. 3—Heat production vs. temperature differential for *T. a. acanthion* (closed circles) *T. a. aculeatus* (crosses) and *T. a. setosus* (open circles) derived from data in Figs. 1 and 2 for FIRST exposure to T_a 20, 15, 10 and 5°C .

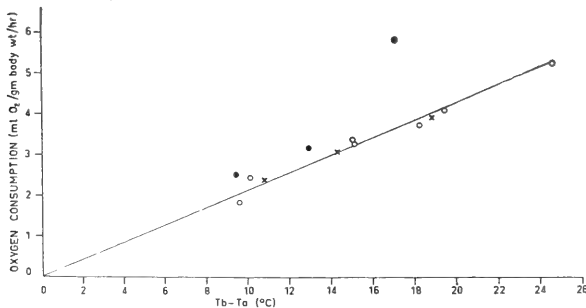


FIG. 4—Heat production vs temperature differential for *T. a. acanthion* (closed circles) and *T. a. aculeatus* (crosses) derived from data in Figs. 1 and 2 for SECOND exposure to T_a 10, 15 and 20°C . Data for exposure of *T. a. setosus* (open circles) to both exposures is shown.

ECHIDNA PELAGE VARIATIONS

difference between the three subspecies. The slope of the line of best fit for all the data in Fig. 4, adjusted for the 'mean' echidna, gives a value of $0.17 \text{ cal/cm}^2/\text{hr}/^\circ\text{C}$. This is in close agreement with the published value cited above of $0.15 \text{ cal/cm}^2/\text{hr}/^\circ\text{C}$.

The difference in conductance between the three subspecies present upon first exposure to decreasing T_a has been removed with acclimation. The values for ALL exposures of *setosus* have been included in Fig. 4, and there is no significant difference between values obtained on first exposure and values obtained on second exposure of this subspecies. Therefore there is no observable acclimation effect in *setosus*, and the effect of acclimation on the other two subspecies has been to bring them to the conductance level of *setosus*. This is not due to increased heat production, since oxygen consumption of *acanthion* and *aculeatus* decreased upon second exposure. It must therefore be due to decreased heat loss or, conversely, increased insulation. On outward appearance the initial differences in insulation could be due to the marked differences in pelage. However, there were no observable changes in pelage after the period of acclimation. Other structural changes, such as in subcutaneous fat storage, could have occurred. Changes in insulation can also be brought about by circulatory adjustment, increased peripheral constriction leading to decreased heat loss. Although circulatory adjustments have been described in acclimation of many mammals, this has not been directly demonstrated in echidnas and little is known about blood flow and circulatory control in monotremes.

Results of this study show that long term phenotypic differences in echidnas can be altered by acclimation. They also highlight the importance of acclimation in temperature regulation studies. Perhaps some of the differences in published T_b and metabolic levels in monotremes relate to unpublished differences in acclimation due to the different conditions under which the animals were kept prior to the studies being made.

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Monotremes and the Evolution of Homeothermy

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MONOTREMES ARE HETEROTHERMS

In this review I shall consider the term 'heterotherm' to apply to an endotherm that shows considerable variation in body temperature (T_b) over short time periods — particularly circadian. This encompasses what has been termed daily torpor in small rodents (Morhardt 1970) but does not encompass hibernation. Obviously the decision as to what constitutes 'considerable' T_b fluctuations is relative. Even the best known homeotherms, including man, have some circadian T_b variations. In general, the greatest diurnal variation in T_b occurs in the smallest mammals (Hudson 1965). The picture seems to be the same in small birds such as hummingbirds (Calder and Booser 1973).

The degree to which T_b fluctuates in heterotherms depends largely on the differential between peak T_b and ambient temperature (T_a). In echidnas with temperature-sensitive radio transmitters implanted in the peritoneal cavity, T_b fluctuated at most 2°C when the animals were kept at T_a 25°C (Fig. 1). However, the same echidnas kept at T_a 10°C showed fluctuations as much as 10°C (Fig. 2). All three animals shown in Fig. 2 are adult echidnas, weighing 4.5 kg. I know of no eutherian or metatherian mammal of similar size which shows this degree of heterothermy. The heterothermia of echidnas is not to be confused with hibernation. As long as sufficient food is available for them to maintain normal body weight, echidnas will survive indefinitely at T_a as low as 5°C with no visible signs of torpor (torpor being a state of dormancy wherein T_b is close to T_a and metabolic functions are at a low level). An echidna with T_b as low as 22°C has no visible difference from one with the 'normal' T_b of 32.5°C. They move about and feed, although such activities soon lead to increased T_b .

MONOTREMES DEPEND ON SHIVERING THERMOGENESIS

The low body temperatures shown in Fig. 1 and 2 were recorded at times when the animals were inactive, while the peaks in T_b correspond to periods of activity. In fact the T_b of an active echidna is highly predictable; it is about 32.5°C regardless of T_a . This was borne out in studies under natural winter conditions in which echidnas with implanted transmitters were found, upon returning to their nesting boxes where radio signals could be monitored, to have active body temperatures around 32.5°C (Fig. 3). When they left the nesting boxes (usually mid-morning) T_b had dropped 4 or 5 degrees.

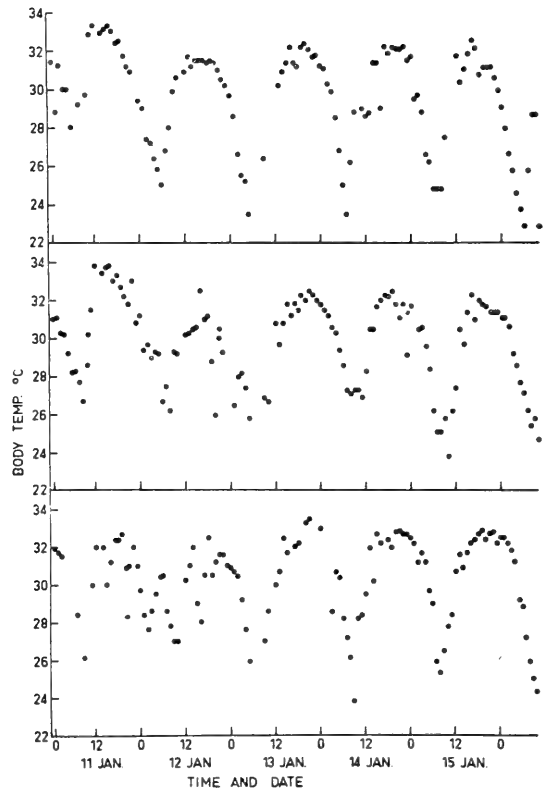
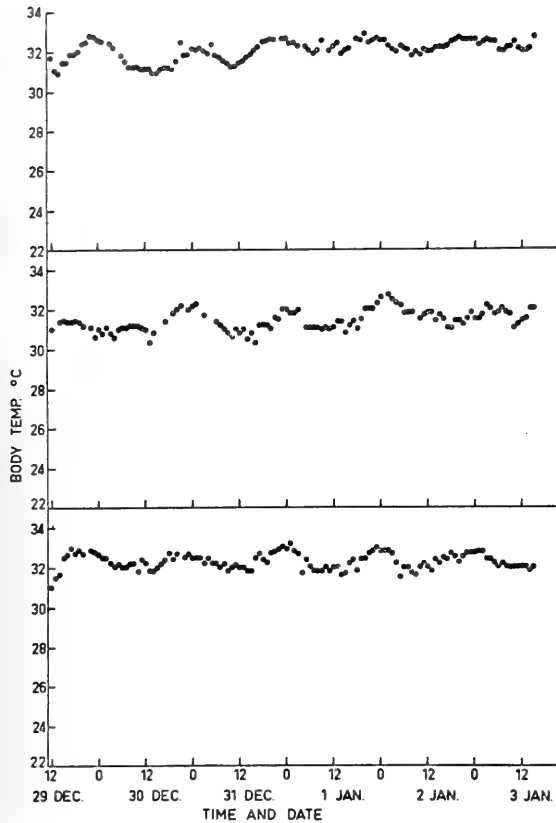


FIG. 1.—Body temperature of three adult echidnas monitored by temperature-sensitive radio transmitters in the peritoneal cavity. T_a is 25°C throughout.

FIG. 2.—Same animals and same conditions as Fig. 1, except that T_a is 10°C throughout.

The importance of activity and striated muscle as a heat source is further illustrated by the effect of 'Flaxedil' (gallamine triethiodide, May and Baker Australia). A normal echidna taken from room temperature and placed at 5°C will not become torpid for several weeks even though food is withheld. If 'Flaxedil' is administered via a venous cannula until muscle tonus is lost but breathing remains normal (dose is about 2 mg/kg), and the animal is then placed in a 5°C room, it cools immediately (Fig. 4). As indicated by the arrow in Fig. 4, when the animal is returned to room temperature it rewarms and survives. One animal treated in this manner was left in the cold room until T_b reached T_a 5°C and did not recover. Since the primary action of 'Flaxedil' is the same as curare (i.e.

MONOTREMES AND HOMEOTHERMY

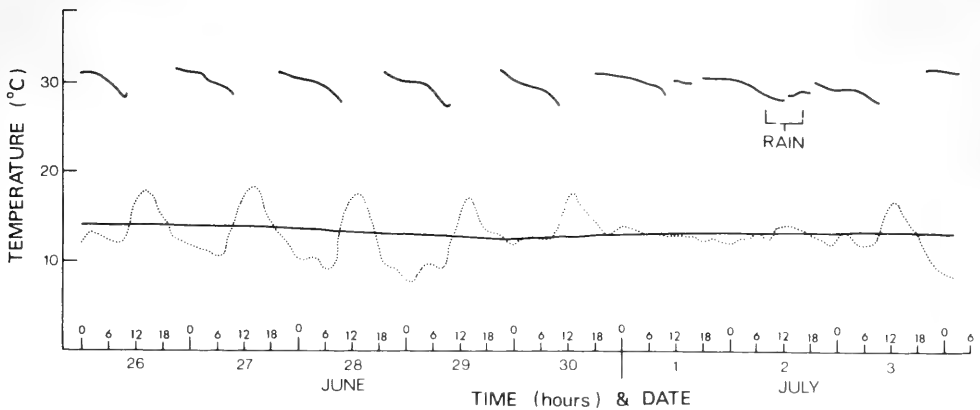


FIG. 3.—Body temperature of an echidna (broken solid line), air temperature (dotted line) and ground temperature (solid line) during natural winter conditions in Melbourne, Vic. Body temperature signals from an implanted radio-transmitter could only be received when the animal was in its nest box.

it depolarises the myoneural junction), the total inability of the treated echidnas to resist passive cooling highlights the essential role of striated muscular activity as a heat source.

Similar data is not available for platypus, although there is some evidence that when their movement is restricted platypus are unable to hold their body temperature at the 'normal' active level in cold water. Smyth (1973) confined platypus in small chambers containing cold water (T_a 9–11°C), and after 15 or more minutes he found T_b to drop as much as 12°C. Grant and Dawson (1978) found that platypus trapped in nets (and therefore restrained) in streams in winter in N.S.W. had body temperatures significantly lower than those of platypus netted in the same locations in summer. However, in laboratory studies using radio telemetry they found platypus to maintain T_b between 32.0 and 32.5°C in water at temperatures from 5 to 25°C. The platypus in these studies were unrestricted and free to leave or enter the water at will. When the platypus were resting in air, Grant and Dawson (1978) found T_b to be 32.0 to 32.5°C at air temperatures from 5 to 25°C. No information was given about the length of exposure to various air temperatures or the relationship to activity. Lacking such information, it is only possible to state at this time that platypus appear to hold a more constant T_b than echidnas, perhaps related to the high degree of insulation provided by the fur of platypus.

The fall in T_b of inactive monotremes at low T_a indicates minimal heat from non-shivering thermogenesis (NST). Brown fat is an important site of NST in many animals, but I have been unable to find brown fat in echidnas after careful

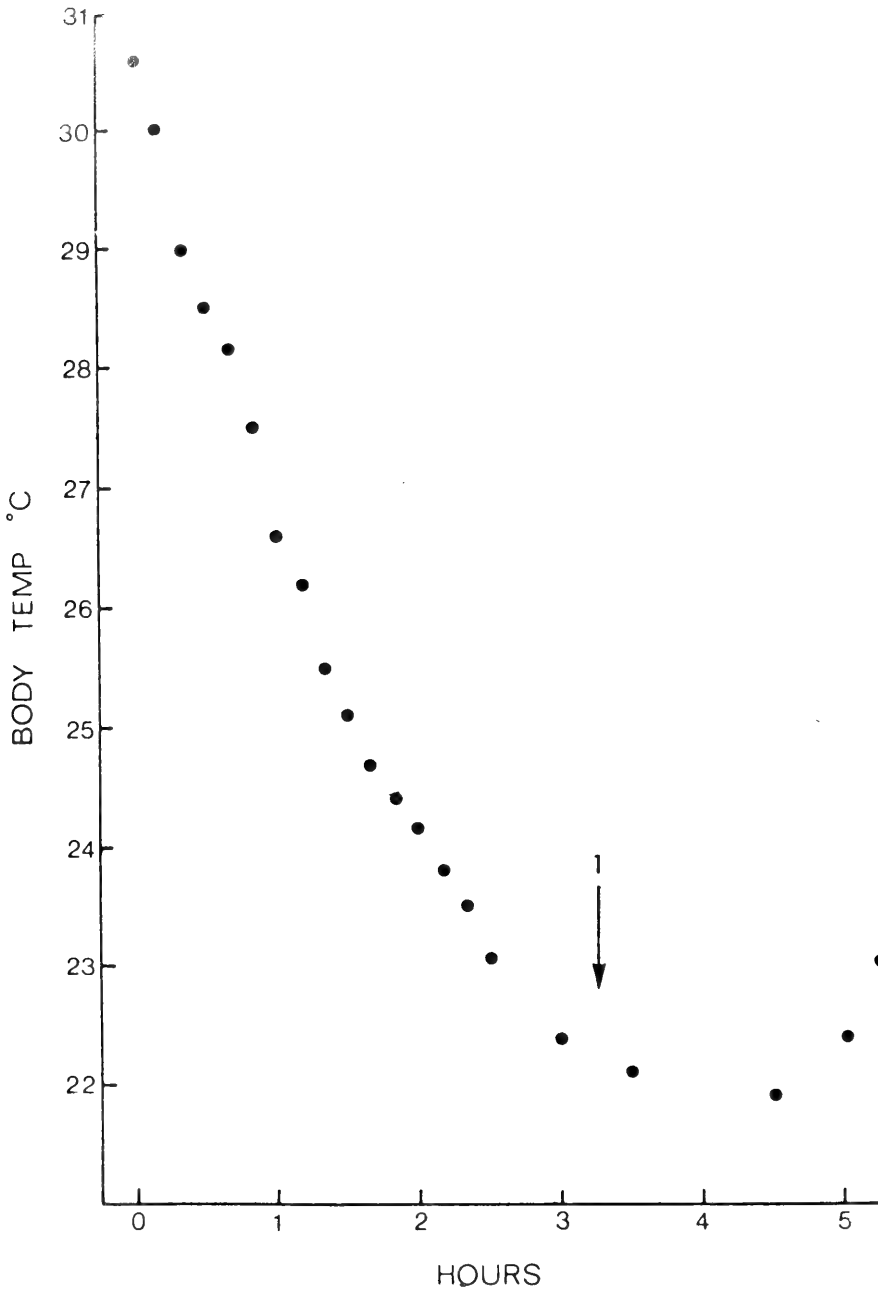


FIG. 4.—Changes in T_b in an echidna treated with “Flaxedil” and placed at T_a 5°C at time 0. The arrow (1) indicates when the animal was returned to room temperature.

MONOTREMES AND HOMEOTHERMY

histological examination of adipose tissues. The low level of NST is further indicated by the low level of oxygen consumption of inactive monotremes. Dawson (this volume) has shown very low levels in the New Guinea long-beaked echidna *Zaglossus*. Oxygen consumption is at its lowest in inactive *Tachyglossus* at about T_a 25°C. Under these conditions oxygen is consumed at about 0.15 ml/gm body weight/hour. This is about one third the level predicted for eutherians of equal weight based on the factor $3.42 W^{-0.25}$ (Augee 1976). This value does not allow for differences in T_b between echidnas and eutherians. A few metabolic measurements obtained under experimental conditions on echidnas with T_b near 38°C do give higher values which are approximately 70% that predicted for eutherians (Augee 1976).

MONOTREMES ARE NOT HIBERNATORS

As long as echidnas are supplied with sufficient food they resist torpor regardless of T_a (Augee *et al.*, 1970). In all instances of reported torpor in echidnas there is evidence that, generally due to an inappropriate diet, the animals were in a condition of weight loss. The prime evidence cited as support for monotreme hibernation is a paper by Wardlaw (1915). However, he states that his animals were "rather emaciated", and most appear to have weighed less than 2 kg on capture. Wardlaw (1915) did observe periods of torpor lasting from one to seven days. However, of his seven animals, three did not recover from their first torpor and died without rewarming. Three others became active after one bout of torpor, became torpid a second time and then died without rewarming. The last animal survived, but it is unclear if it ever became torpid. Hibernation is generally

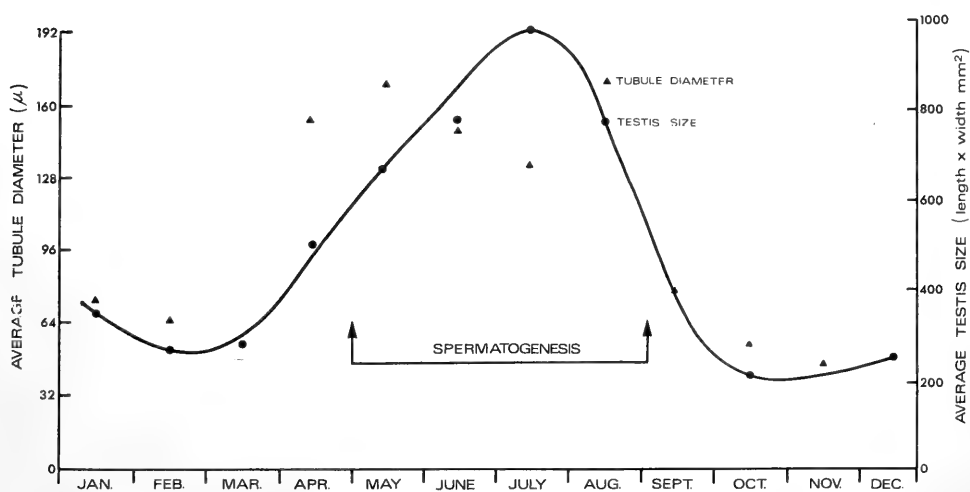


FIG. 5.—Season reproductive changes in male echidnas. Figure from Wendy Baldwin.

considered to involve a controlled, adaptive use of torpor as an energy conservation method. The condition described by Wardlaw (1915) certainly conserves energy, but it does not appear to be highly adaptive.

True hibernation is a seasonal phenomenon. The mammal is homeothermic for much of the year, and during that period the breeding season (or at least the mating season) occurs. There is no hibernator in which the mating season and hibernating season occur at the same time. Yet it is clear, from data such as that gathered by Wendy Baldwin for testis cycles (Fig. 5), that the breeding season of echidnas begins in June with mating at its peak in July. This is, of course, mid-winter in Australia. There is also no apparent seasonal pattern in resistance or susceptibility of echidnas to torpor. If food is available, they will not become torpid at any time of the year regardless of T_a . Likewise, if they do not have sufficient food to maintain body weight, they will eventually become torpid at any time of the year. Seasonal investigations of the histology of the thyroid and adrenal glands have revealed no seasonal changes. There is, of course, as indicated by Fig. 5, marked seasonal variation in gonadal size and function.

THE RESPONSE TO LOW T_a IS TOLERANCE

A drop of T_b as great as 10°C does not seem to interfere with normal function in echidnas. Echidnas faced with low T_a allow T_b to fall, even though they have the capacity to increase heat production. As shown previously (Augee, 1976), they can increase their basal metabolism by more than three times thermoneutral levels upon exposure to T_a 5°C . Those values were obtained from echidnas that were not active, and the heat source was presumably shivering. But, whatever the heat source, it is clearly not utilized to prevent declining T_b at least to T_b levels around 22°C , when echidnas are at rest at T_a 10 - 20°C . Echidnas simply tolerate the low T_b . Even when forced by starvation and low T_a into repeated bouts of torpor, from which they are unable to arouse themselves, they will withstand repeated cycles of torpor and rewarming by the application of external heat (Augee and Ealey, 1968).

THE RESPONSE TO HIGH T_a IS AVOIDANCE

Monotremes have little tolerance for elevated T_b (Augee, 1976). Echidnas do not pant, salivate or sweat in response to heat. The platypus has the same low tolerance to heat and elevated T_b (Robinson, 1954), yet they possess abundant sweat glands (Montagna and Ellis 1960) which produce sweat even with a slight elevation of T_a (Augee 1976). The functional significance of this is obscured by the fact that platypus are semi-aquatic animals found only in the relatively temperate coastal regions of Australia, including Tasmania.

Captive echidnas (Augee *et al* 1970) and echidnas tracked in the wild with radio-telemetry (Augee *et al* 1975) avoid air temperatures much above 32°C , either by limiting their activity to appropriate times of the day or by seeking

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shade. Problems of over heating would be increased by the added heat load of increased muscular activity, but neither monotreme type depends on escape for defence. Echidnas when disturbed dig into the earth, so that only the dorsal spines are exposed, and platypus dive or take refuge in their burrows.

MONOTREMES AND THE EVOLUTION OF HOMEOTHERMY (AND ENDOTHERMY)

Modern therian mammals are homeothermic and endothermic. In addition, the level of body temperature is high, approaching 40°C. Endothermy is not automatically a prerequisite for homeothermy. As McNab (1978) pointed out, animals in a thermally constant environment (like the sea) are trivially homeothermic. More important in vertebrate evolution, a very large animal may be homeothermic by virtue of the thermal inertia and favourable body mass to surface ratio resulting from its size. Such animals have been aptly termed "inertial homeotherms" by McNab and Auffenberg (1976). Further, for an animal whose primary source of heat is the activity of striated muscle, bulk is a distinct advantage (Friar *et al* 1972). It is likely that many of the Mesozoic reptiles, particularly dinosaurs, achieved homeothermy (with a high T_b and consequently a high level of metabolic activity) by this strategy. They were not necessarily endotherms. Bulk does not seem to have been the strategy in the therian lineage. From the late Triassic to the late Cretaceous, fossils with the mammalian jaw articulation are the remains of very small animals (Jenkins and Parrington 1976). Clearly the thermal strategy in the mammalian line of evolution at that period did not depend on bulk, although it might well have resulted in a T_b above air temperatures because of a decreased thermal conductance resulting from fur. The fur of all living mammals, including monotremes (Romer 1897), is much the same, and McNab (1978) has suggested that a fur coat might well have preceded mammals (an evolutionary stage defined by the jaw articulation) by as much as 35 million years.

In 1964 Cade proposed four evolutionary stages between ectothermy and the endothermic homeothermy of modern therians. Stage 2 of his scheme proposed that the "first thermogenic mechanisms were associated primarily, and perhaps at first exclusively, with muscular activity. This primitive endothermic ability allowed the animals to function for longer periods of time over a greater range of ambient conditions at the preferred upper end of their zone of thermal tolerance, but they still retained tissues adapted to survive cooling periods of inactivity, or when ambient conditions overpowered their limited ability for heat production". Cade thought no living animals represented this stage, but on the basis of the above discussion I suggest that monotremes fit it very well. In addition, the above ideas suggest that animals with such levels of thermogenesis are heterothermic, with a low T_b around 32°C during activity. McNab (1978) proposes that homeothermy preceded endothermy in the mammalian lineage and suggests that endothermic homeothermy was achieved by the very small animals (Mesozoic mammals)

evolved from the late cynodont lines. Living monotremes are, of course, considerably larger than the fossil mammals prior to the late Cretaceous. However, McNab (1978) suggests that some of the larger late cynodont lines had "intermediate (poor) endothermy", and it seems logical that the living monotremes are remnants of that stock.

If the low level of T_b (around 32°C) in active monotremes is representative of the early mammalian lineage, what has led to the much higher T_b of both marsupials and placentals? In a recent review of the evolution of homeothermy in mammals, Crompton *et al* (1978) suggest that body temperatures approaching 40°C are essential for small homeotherms that are diurnal and encounter solar radiation. This would explain the acquisition of high T_b by the small mammals that were ancestors to the therians. In my view monotremes are not on that line of evolution. Crompton *et al* (1978), however, do not believe this and propose that monotremes arose in the Cenozoic from diurnal ancestors with "mammalian-type energetics". They assume monotremes to be homeothermic and state that they are nocturnal animals that regulate their body temperatures "while resting at night at about 30-35°C". This is clearly not the case (see Fig. 2), except at thermo-neutral T_a . Nor do monotremes have "mammalian-type energetics" if one considers their resting metabolism. Crompton *et al* (1978) make their comparisons between lizards, monotremes, marsupials and insectivora on the basis of exercising metabolic levels. In my opinion this is irrelevant. I believe that heat production from the activity of striated muscle, coupled with various methods of decreasing conductance, as a means of thermoregulation goes back much further in vertebrate phylogeny than the origin of mammals, or even the origin of therapsids. An important step in the evolution of therian homeothermy, essential for maintenance of high T_b at rest, was the acquisition of high levels of non-shivering thermogenesis. Monotremes have very little NST capability. Presumably there is a certain level of heat production in all monotreme tissues, as there must be in all living cells that depend on exothermic oxidative pathways, but that heat cannot maintain body temperature at low T_a . It is the acquisition of additional NST ability (often termed facultative NST) that sets the therians apart from the monotremes and makes possible homeothermy as opposed to heterothermy. Facultative NST would have been highly advantageous for the therian ancestors if they were small homeotherms with high body temperatures.

Unless fossil evidence is obtained to the contrary, the best interpretation of monotremes in regard to mammalian endothermy/homeothermy is that they represent an early stage in its evolution. The living monotremes can best be regarded as remnants of the medium to large sized late cynodonts and part of a lineage separate from the small Mesozoic mammals ancestral to therians.

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Observations on Behaviour of Echidnas at Taronga Zoo

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ABSTRACT

Even when presented with a spacious and complex environment, echidnas grouped together in preferred sites and were mutually tolerant. In paired encounters at feeding sites no evidence could be found of territorial behaviour or of a hierarchy based on size. There was a dominance hierarchy among animals of the same sex, but the basis is unknown. During the study a birth occurred. Conclusions are presented regarding housing of echidnas in zoo displays.

INTRODUCTION

Little is known about social behaviour in echidnas. Brattstrom (1973) studied confined echidnas and reported a loose hierarchy based on size. His conclusion was based on behaviour of about 30 echidnas housed together in one pen which lacked any natural features, containing only the echidnas and a thin layer of sawdust on the floor. In nature echidnas are rarely found together, although small groups have been reported during the mating season. A group of five males, with one female, was reported in Victoria in early August (Augee *et al*, 1975). For most of the year echidnas are solitary, with large overlapping home ranges (Augee *et al*, 1975), which suggests the possibility of territorial behaviour. In order to investigate possible territorial behaviour, and to re-examine social behaviour under more natural conditions, the present study was conducted in a large enclosure at Taronga Zoo, Sydney. The enclosure was exposed to natural weather and light conditions and presented a complex environment with ample opportunity for spatial segregation and for experimental manipulation of spatial organization.

Breeding of echidnas in captivity is very rare and has only been reported once in Berlin (Heck, 1908) and twice in Basel (1955 and 1967, E. Lang pers. comm.). During the course of this study a pouch young was found, indicating that the conditions under which the animals were housed was conducive to copulation, conception and rearing of the young almost to independence.

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10 m

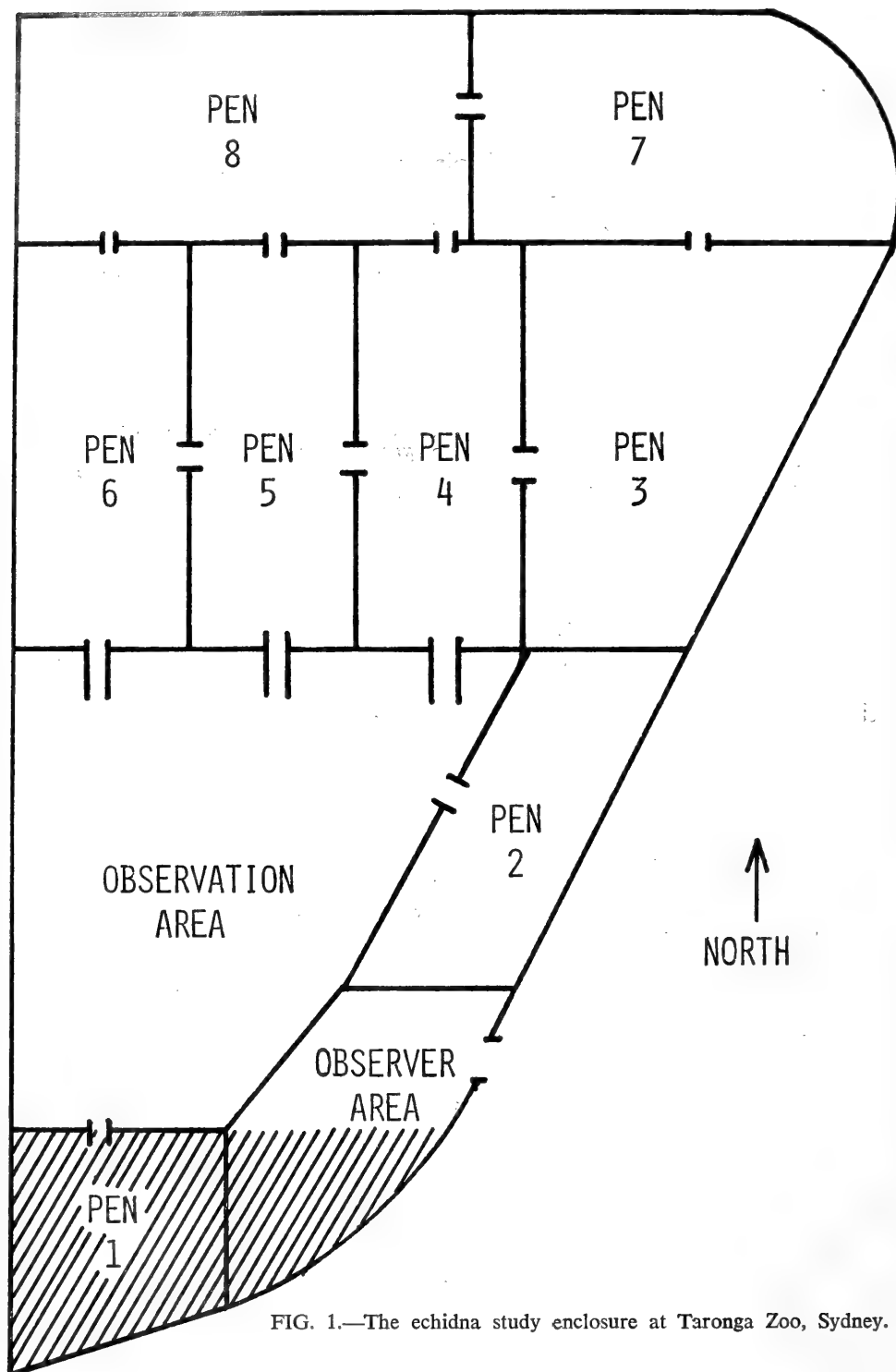


FIG. 1.—The echidna study enclosure at Taronga Zoo, Sydney.

ECHIDNA BEHAVIOUR

MATERIALS AND METHODS

The echidnas used in this study were adult animals of the nominate subspecies, *Tachyglissus aculeatus aculeatus*. The sex and weight of each animal is shown in Table 1.

TABLE 1
ECHIDNAS HOUSED IN THE ZOO ENCLOSURE

Echidna number	Sex	Body weight (gm)
T1	F	4950
T3	M	3850
T4	M	2200
T5	M	8400
T6	F	4950
T7	F	5300
T8	F	6600

The echidnas were fed each afternoon between 1400 and 1600. The diet, which has been used successfully at Taronga Zoo for many years, consisted of: minced meat, yoghurt, egg yolks, condensed milk, dicalcium phosphate, multivitamin drops and vitamin E. There are no advantages known to us of such a complex diet compared to the much simpler diet reported by Augee and Ealey (1968). Diets for adult echidnas which contain milk invariably cause diarrhoea and subsequent weight loss, presumably due to the lack of the enzyme lactase in adult echidnas (Kerry, 1969). While the Taronga diet overcomes this by the addition of yoghurt (which contains lactase), it seems simpler to eliminate milk. The diet of Augee and Ealey (1968) has the further advantage of not spoiling readily if left in feeding dishes.

The enclosure at Taronga Zoo is shown in Fig. 1. It had an area of 174.5 m² and was surrounded by a concrete wall about 1.8 m high. Zoo visitors could pass along all walls except the west side, which was adjacent to another animal enclosure. As indicated in Fig. 1, there was a concrete roof over pen 1 and part of the observer's area. The enclosure was subdivided into 10 sections; with one area for the observer and equipment, a large "observation area" originally intended for observation of group behaviour, and eight pens. The eight numbered pens, except for pen 1, contained nesting boxes, sections of pottery pipe, grass clumps, pieces of log and a covering of soil. The soil was at least 15 cm deep in pens 2-8. Pen 1 contained straw, with some sawdust and soil as floor covering. The inner walls were cement brick 1 m high.

Access between pens could be controlled by doorways, the positions of which are indicated in Fig. 1. The doorways were large enough to allow an echidna to pass without touching the sides. Wooden doors could be bolted across the doorways to prevent passage.

RESULTS

WITH OPEN ACCESS TO ALL PENS

Animals tended to group together throughout the study when free access was allowed. At the time of first daily observation (0830-0900) made on 20 different days between 2 June and 21 July, a mean of 51.5% of the echidnas observed were grouped. Pen 1 was preferred. In these observations all but one of the echidnas were found in pen 1 more than 10 times. The exception was T3,

and that animal was only found in pen 1 five times. Echidnas in pen 1 were grouped in one particular corner 69% of the time (mean of individual locations over 20 observations of pen 1). The composition of the group frequently changed, but the focus did not. The corner used was the only place in the entire enclosure not readily visible to zoo visitors passing on either side of the enclosure, and it was also in the path of morning sun rays in winter.

Each pen was furnished with a wooden nest box measuring 78 x 57 cm, and either 34 or 63 cm high. A half circle 12.5 cm in radius was cut out of one side of the box at ground level for access. In all, these boxes appeared to humans to be very fine places for echidnas to overnight but had no such appeal for the subjects. They occasionally entered them, but not a single echidna was known to spend a night in one. However, they were used in another way, particularly during winter when the most common resting site was a hollow excavation *under* the box. When the boxes were moved, new excavations were made under them the same night. Pottery sewer pipes, 1 m in length and about 40 cm in diameter, were also placed in the pens. Echidnas are known to occasionally use hollow logs in the wild (Augee *et al.*, 1975). Echidnas went in and through them, but again no echidna was ever observed to overnight in one. An attempt to make the pipes more "log-like" by closing one end with a hessian bag had the same result, although one echidna was observed resting inside one of the bags.

The dirt covering of the pens was in most areas deep enough to allow the construction of burrows. Six burrows were constructed in winter (June-July) and one in the spring. Three of the burrows were constructed by the same echidna (T3). The burrows ranged from 3 to 18 cm deep and the longest was 35 cm. It is not possible to state how often the burrows were used nor how many individuals might have used a given burrow, as the complexity of the environment provided made it impossible during winter to know the position of every animal at every observation.

Resting sites, here defined as the position of an inactive echidna observed at anytime during daylight, were almost always dish-shaped excavations or hollows, as described by Griffiths (1968). Usually these excavations were deep enough so that only the dorsal spines were visible. Regardless of the fact that most observations were made during the winter (air temperature on 42% of the observations was below 18°C), resting sites were almost always (82%) in the shade. We cannot relate this to temperature preference or temperature regulation, since we have no way of evaluating the degree to which choice of resting site was related to avoidance of zoo visitors. However, the finding has practical implications for the display of echidnas in zoos.

WITH CONTROLLED ACCESS BETWEEN PENS

Animals were confined to individual pens for 18 days from 21 July. After that the doors between pens were opened at feeding times to allow interaction

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between selected pairs in adjacent pens. Since the above observations showed that there was little social interaction between echidnas, even when grouped, encounters were encouraged by placing the food for each pair in one of the pens (the "home pen") for a limited time. The following scheme was used to score encounters between two echidnas at the feeding dish. The encounter of the subject echidna with another was scored as a:

LOSS if

- (a) it was displaced from the feeding dish by the other;
- (b) it approached the feeding dish, but waited until the other echidna had finished eating before it fed;
- (c) it approached the feeding dish and ate only after the other echidna had eaten and left.

WIN if

- (a) it approached the feeding dish and displaced another echidna already eating;
- (b) it finished eating and was not displaced by another echidna which had approached the feeding dish;
- (c) it ate first, while another echidna waited before approaching the feeding dish.

DRAW if both animals ate together.

TABLE 2

OUTCOMES OF FEEDING ENCOUNTERS BETWEEN PAIRED ECHIDNAS

a. Comparison by home pen—the echidna in the home pen being the one in whose pen the food was placed.			
	Win	Loss	Draw
In home pen	15	14	13
Out of home pen	14	15	13
b. Total number of wins, losses and draws scored by males and females.			
	Win	Loss	Draw
Males	15	12	9
Females	28	10	10
c. Comparison of encounters with opposite sex and with same sex.			
	Win	Loss	Draw
Male with female	10	9	26
Male with male	6	6	0
Female with female	12	6	0
d. Total number of wins, losses and draws scored by size comparison.			
	Win	Loss	Draw
Small (T4)	7	2	3
Medium (T1, T3, T6, T7)	22	9	17
Large (T5, T8)	0	18	6

Encounters were first examined in terms of "home" pen, the home pen being that in which the animal had been confined by itself for 18 days. In Table 2a; win, loss or draw in home pen refers to the encounter results for those echidnas in whose pen the food was placed. Win, loss or draw for the "out of home pen" animal refers to that echidna who had to go into an adjacent pen to feed. There is no significant difference in the encounter result, whether the subject echidna was in its home pen or in an adjacent pen ($\chi^2 = 0.069$, 2 df.). In other words, an animal in its home pen did not necessarily score a win in the feeding situation. Furthermore, after feeding, the animals usually paced between pens. If the doors were left open for 2-3 hours, until they had selected a resting site, there was no discernible pattern in whether the home pen or the adjacent pen was selected, nor in whether the two echidnas were in the same or separate pens.

The same 42 encounters between pairs were examined to determine if males differed from females in the results of encounters (Table 2b). There was no significant difference in outcome between males and females in opposite sex encounters ($\chi^2 = 2.502$, 2 df.).

However, a significant sex-related difference in encounter results is seen when encounters of animals of the same sex are compared with encounters of animals of opposite sex (Table 2c). There were significantly greater numbers of wins and losses scored in the former than in the latter ($\chi^2 = 28.366$, 6 df $\alpha < 0.001$). That is, when animals of the opposite sex were paired, they usually ate together (a draw). When animals of the same sex were paired, there was always a win or loss. However, displacements at the feeding dish were never the result of aggressive behaviour. If feeding when the other echidna approached, the animal scoring the "loss" moved away from the dish with a jerk and either remained close by with its head under its body or walked about (often between both pens) until the other had finished.

TABLE 3
RESULTS OF ENCOUNTERS BETWEEN PAIRED ECHIDNAS

	T1	T3	T4	T5	T6	T7	T8
T1	*	0	+	—	+	—	—
T3	0	*	—	—	0	0	—
T4	—	+	*	—	0	0	—
T5	+	+	+	*	0	+	0
T6	—	0	0	0	*	—	—
T7	+	0	+	—	+	*	—
T8	+	+	+	0	+	+	*

For each encounter scored, the echidna at the top of the column was in its home pen.

 + means the echidna in home pen scored a win in the encounter.

 — means the echidna in home pen scored a loss in the encounter.

 0 means a draw was scored and the echidnas ate together.

Is there a hierarchy within the animals of the same sex? If there is, the results of Brattstrom (1973) suggest it might be on the basis of size. Table 3 sets out all the results of encounters between individual animals. Between males, T3 always won and T5 always lost. Therefore a dominance hierarchy $T3 > T4 > T5$ could be constructed. However, this is not a clear function of weight, since $T3 = 3850$, $T4 = 2200$ and $T5 = 8400$ gm. For encounters between females, a hierarchy $T6 > T1 > T7 > T8$ can be constructed from Table 3. If anything this is the inverse of dominance by size as $T6 = 4950$, $T1 = 4950$, $T7 = 5300$ and $T8 = 6600$ gm. Leaving aside the question of sex, examination of all encounters by size (Table 2d) shows that size does have a significant effect on outcome $\chi^2 = 28.7125$, 4 df. $\alpha < 0.001$). However, this effect is not as Brattstrom predicted, large over small. The smallest echidna, T4, had more wins than expected by chance, while the animals of the large group had less wins than predicted by chance.

REPRODUCTION

A dead pouch young was found on 2 October in the pen with female T7. It weighed 250 gm and measured 11.8 cm along the dorsal curvature from the tip of the tail to the tip of the snout. The spines were just visible, having only barely erupted from the skin surface. It is not possible to state the exact time of death, but the lack of decomposition and the slight desiccation indicated it had probably been dead no more than two days. T7 had a well developed pouch, which rapidly regressed.

It is interesting that the only instance of aggressive behaviour noticed in the entire study occurred between the female that produced the young (T7) and another female (T6) at a time when T7 was probably carrying the pouch young. Five days before the dead young was found, T7 and T6 were in adjoining pens, with the access door open. T7 entered the "home pen" of T6 and, after sniffing T6, placed its snout under T6 and pushed it across the pen. T6 assumed a defensive position (Brattstrom, 1973), with its head under its body. T7 continued to push under T6 until T6 was only touching the ground with its left legs. At this stage T7 walked away, and T6 followed sniffing towards the reproductive female. Twice more T7 put its snout under T6 for several minutes and then walked off, followed by T6. The situation was then reversed, with T6 pushing its snout under the reproductive female, which attempted to turn away. Each time T6 moved to another side of T7, the latter turned her back and presented her dorsal spines or tried to place her snout under T6. This continued for about 10 minutes, after which time T7 walked off. It is of course possible that during this encounter, or a similar encounter, the pouch young of T7 was injured or dislodged, although there is no direct evidence.

DISCUSSION

The results of feeding encounters do not support a simple size-related dominance order as suggested by Brattstrom (1973). While some sort of hierarchy

between animals of the same sex is indicated, it is not at all clear what forms the basis of the hierarchy. On only one occasion was behaviour observed that could be described as aggression, and that occurred between two females, one of which was carrying a pouch young. The encounter did not consist of bumping, as described by Brattstrom, but involved pushing by both animals, with each attempting to push its snout under the other's body.

It is possible that smell is important in social organization of the echidna, and perhaps forms the basis on which hierarchy is constructed. Dobroruka (1960) has suggested the cloacal glands of the female might be used in attracting males for copulation, and Brattstrom (1973) described mutual sniffing of the axillary region.

This study has shown that echidnas are mutually tolerant and readily group to take advantage of favourable positions in the environment of captivity. Although given ample opportunity to establish territories, they did not do so and exhibited no behaviour that could be considered "territorial".

Some specific comments can be made in regard to the housing of echidnas in zoo displays. This study clearly shows that echidnas can be kept in groups without any mutual aggression. Since there was no evidence of pair bonding (the female that had the pouch was observed in groups with several males during the period when copulation probably took place), it is probably not necessary to pair and segregate echidnas for breeding, although it might be advisable to segregate females thought to have mated or to be carrying a pouch young. Echidnas avoided the use of nesting boxes and pipes, but preferred to excavate a shallow depression under some object. When doing so they are only partly visible. However, if a shaded area is provided near the point of observation, there is considerably greater chance of their being visible than is the case with the usual arrangement of open area near the observers with shelter and shade at the rear. We are unable to account for the failure of the mother to carry the pouch young to the stage of independence. It has been suggested that the observed loss of pouch young in captive echidnas is due to the unsuitability of sawdust or other unnatural substances as substrate, but that could not have been the case here. Perhaps there are dietary factors, and we are of course unable to determine whether the young died and was cast out of the pouch, or if it was cast out of the pouch and then died. On two occasions (M. Augée unpubl.), when echidnas with pouch young have been brought into captivity and (their condition being unknown) kept in cages with sawdust on the floor, the pouch young were found discarded but alive. These young subsequently died when attempts to get the mother to take them back failed. Calculating back from the size of the young, and the suggested growth rates (Griffiths, 1968), it is likely the young was hatched about mid-September. Therefore the mother had carried the pouch young for about 20 days. Griffiths (1968) suggests that the pouch young are cast out of the pouch at about 20 days post hatching, when the spines are beginning to emerge. There is sufficient evidence to indicate that, after casting the young from the pouch, the mother leaves the

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young in a burrow, returning occasionally to suckle it (evidence discussed by Griffiths, 1968, pp. 202-203). However T7, the mother, was never observed to dig a burrow, so perhaps conditions were not right for construction of the proper burrow in her pen. This further indicates the value of keeping captive echidnas in a situation with sufficient soil for burrow construction. An additional benefit is that echidnas are heterothermic (Augee, this volume) and soil provides a good insulation to restrict heat loss from the animal, whether completely burrowed or partially covered in a shallow excavation.

Two obvious areas for further study have emerged from this study. One is the role of diet in breeding, and the other is the role of smell in social behaviour and breeding. Unfortunately the enclosure used at Taronga Zoo has been demolished, so these investigations have ceased for the time being.

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Instrumental Learning in the Echidna *Tachyglossus aculeatus setosus*

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Tasmanian echidnas *Tachyglossus aculeatus setosus* were tested in serial discrimination-reversal tasks, comparing their operant behaviour in reversal-shift and non-reversal shift conditions, using positional and visual/tactile cues. Learning set formation of the pattern characteristic of eutherian mammals was observed in all tests for all subjects, but performances were superior in tests of positional discrimination and in reversal-shift conditions. The results were consistent with available neuroanatomical information and suggest more efficient mechanisms of organising relevant stimuli than would be predicted on the basis of the phylogenetic status of monotremes.

INTRODUCTION

Few experimental studies have been made of processes of learning in non-eutherian mammals. Marsupials have been neglected and are consequently often considered to be dull and behaviourally homogenous (Kirkby, 1969). These views are unsubstantiated by critical laboratory tests (Buchmann and Grecian, 1974). Monotremes represent a unique group of mammals with marked reptilian affinities indicated by skeletal features (Hopson, 1970) and physiological mechanisms, particularly those of thermoregulation and reproduction (Griffiths, 1968). They may be regarded as being more closely related to marsupials than to eutherian mammals (Gregory, 1947), and like metatherian species they have been neglected by ethologists and comparative psychologists. This is surprising, in view of the fact that a considerable amount of information is available about the general biology of monotremes (Burrell, 1974; Griffiths, 1968) and their unique features.

One species of monotreme, *Tachyglossus aculeatus*, has received more attention than any other, yet even this has been the subject of few behavioural investigations. Brattstrom (1973) documented the naturalistic behaviour of the continental subspecies *T. aculeatus aculeatus*, and studies of the learning performance of the latter were made by Saunders and several associates (1971 a,b).

Monotremes are generally considered to be more primitive than marsupials and may, therefore, be expected to be less successful in performing comparable tasks designed to test learning ability. However, the investigations of Saunders

et al. (1971 a,b) demonstrated that echidnas are as capable of forming a position-habit in T-mazes as are laboratory rats, and they showed consistently improving performances similar to those of eutherian mammals. This suggested that further studies on learning in monotremes would yield results of considerable interest.

The present investigation is based on a series of experiments employing repeated reversals of paired instrumental discrimination tasks. At present, no published information is available about the performance of any prototherian subjects in learning situations employing operant techniques. Tests of reversal learning are frequently used in studies of phyletic comparisons (Mackintosh, 1962; Bitterman, 1965, and others).

The results reported below were obtained from tests on Tasmanian echidnas, *Tachyglossus aculeatus setosus*, distinguishable from the nominate subspecies of continental Australia by having fewer spines and a shorter and broader snout, as well as differences in the proportions of the hind-claws and lighter pelage.

METHODS

SUBJECTS AND MAINTENANCE

The subjects used in the investigation were six echidnas, collected from various localities in Tasmania.

It is difficult to determine the sex of an echidna on the basis of its external features because the ankle spur, potentially useful as a diagnostic feature and present in all males, is on rare occasions possessed by females. E2 and E5 were known to be females on the basis of post mortem examination, and the observed presence of well-developed pouch folds, respectively. The sex of the other subjects was not established.

The age of live adult echidnas is also difficult to ascertain with any degree of accuracy because of the unavailability of reliable criteria from field or laboratory studies. Body weights of the subjects are shown in Table 1.

All subjects were exposed to the presence of the investigators and were handled extensively on a daily basis throughout their period of maintenance. They became noticeably tame both in their home-cage situations and subsequently in the experimental arena, but it required a minimum of two-three months to reduce their initial timidity sufficiently for experimentation to commence.

The subjects were maintained on mixture of pollard, meat-meal, glucodin and water, supplemented by vitamins (ABCDE drops, Parke, Davis & Co.). These dietary constituents are adequate to provide the nutritional requirements of echidnas, provided that the mixture is of a porridge-like consistency. If the mixture is too dense the animals may experience difficulties in drawing it into their mouths; if it is too dilute, it may provide insufficient nourishment and have a lower incentive value. In addition to the standard mixture, other types of food, including eggs, yoghurt and orange juice, were occasionally provided. When the subjects were considered to be adequately tamed, and made no escape responses, they were often released for considerable periods to forage for ants in outdoor situations.

Subjects undergoing tests were housed individually for the duration of the tests in wire mesh cages (dimensions: 2 m x 1 m x 1 m); otherwise the animals were housed communally in a single cage measuring 3 m x 2 m x 2 m. This presented no problems, as "pugnacious" behaviour was never observed.

General observations of the animal's behaviour were made in the experimental situation, indoor and outdoor conditions at the Department of Zoology of the University of Tasmania, and in various domestic dwellings.

APPARATUS

All experiments were conducted in a room with neutral grey walls and floor, the latter divided into 0.5 m squares by means of intersecting red lines. These were used to

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monitor the ambulatory activity of the subjects. A feeder with rotating cups was installed behind one of the walls and connected by concealed wires to a pair of electrically-operated treadles. The surface of each treadle measured 15 x 10 cm and consisted of two flat plates. When the latter were depressed with sufficient force (a pressure of 25 g or more) an electric contact was established between them, activating the feeder switch and resulting in food being dispensed into a food trough in the test arena. The treadles were covered with removable Perspex plates and equipped with slots into which cardboard keys, visible through the plastic lids, could be inserted. The treadles were capable of being operated simultaneously or independently and a manual switch was also available for operation by the investigators outside the arena. The animals were observed through a one-way window set in the wall of the room.

Echidnas are commonly active during daylight hours and all experiments were conducted in afternoon sessions. Additional illumination was provided in the observation area by a single 100 W light globe equipped with a red filter.

A diagrammatic illustration of the experimental arena is shown in Fig. 1. The design of the experiments and equipment used in this study are considered to be more suitable for Australian mammals captured as wild specimens than the more conventional Skinner boxes and related types of apparatus and were successfully employed in a previous study using marsupial subjects (Buchmann and Grecian, 1974).

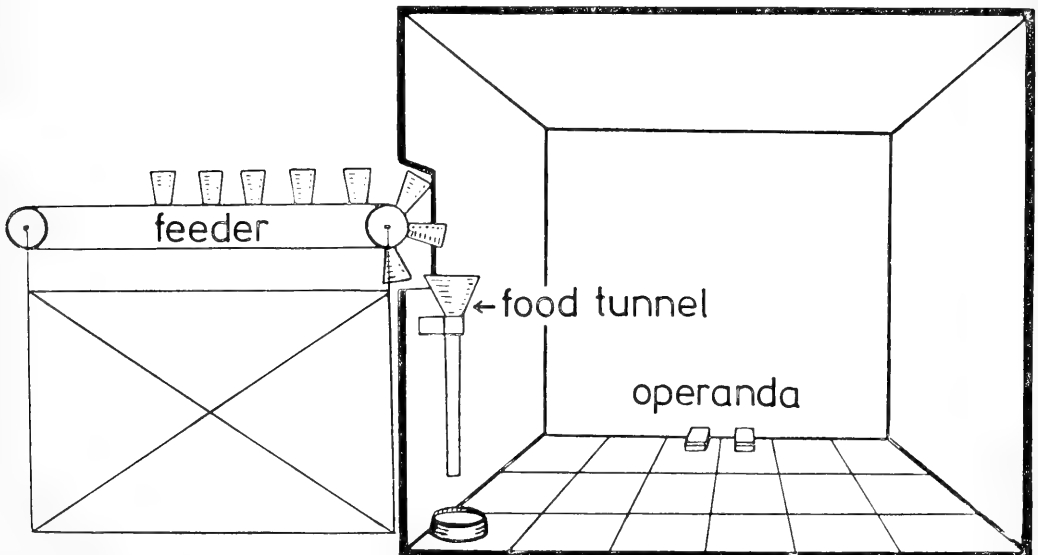


FIG. 1.—Diagram of the experimental arena and equipment used in the investigation. The room dimensions were 3 m x 3 m x 3 m, and the floor was divided into 50 cm squares.

The investigation was based on tests of series of reversal-shift and series of non-reversal-shift conditions. Performances between the latter were compared to assess whether or not improvement occurred in the two types of test situations. Performances within series of reversal shifts ($n=4$) and in series of non-reversal-shifts ($n=2$) were also compared. Two discriminations were involved; one a positional discrimination (left and right) and the other a visual/tactile discrimination (black/rough and white/smooth). Tactile and visual cues were combined in a part of the experiment because vision is not considered to be the

echidna's *forte* (Griffith, 1968). In the tests using reversal-shift conditions, two subjects received positional discrimination choices, and two were presented with visual/tactile discrimination tasks throughout the experiment. In tests involving non-reversal shift conditions, positional and visual/tactile discrimination tasks were alternated throughout each series of tests. Initial discriminations were counterbalanced as far as possible between left and right and black/rough and white/smooth cues. Modified Gellerman sequences were used whenever random ordering was required (Gellerman, 1933).

The reinforcement consisted of food delivered from the feeder apparatus, either following the manipulation of one or both treadles by the subjects or by means of the manual feeder switch operated by the investigators.

Laboratory rats used in similar experiments of learning are generally deprived of food until their body weight is reduced to 85% of their original free-feeding weight. Following experimentation, they are re-weighed and fed an appropriate number of food pellets (Michael, 1963).

All of the echidnas used in this study lost weight after capture, and it was considered that an additional loss of 15% of their weight would be excessive. Attempts were therefore made to ascertain the amount of food required to maintain motivation. This was found to depend on factors such as body weight and the amount of food obtained by the subjects during experimentation. The subjects were weighed each day over a period of two weeks to record pre-feeding weights, and the partially deprived body weight was eventually established to be an average of approximately 88% of the free-feeding weights at the time of capture. The amount of feeding sufficient for maintaining the subjects' weights at this level was compatible with ensuring that they operated the treadles in the experimental situation in order to obtain food, while preventing serious loss of condition.

Table 1 summarises the weights at the time of capture, mean free-feeding weights and mean food-deprived weights of the subjects.

TABLE 1

INITIAL WEIGHTS RECORDED AT THE TIME OF CAPTURE,
MEAN FREE-FEEDING WEIGHTS AND MEAN FOOD-DEPRIVED
WEIGHTS OF THE SUBJECTS.

Subject	Initial weight (g)	Mean free-feeding weight (g)	Mean food-deprived weight (g)
E1	2500	2350	2220
E2	2250	2000	1950
E3	2200	2100	2000
E4	3100	2940	2760
E5	2100	1960	1800
E6	2700	2590	2450

The magazine-training procedures used in this investigation were simple and followed the methods outlined by Michael (1963) in essential details. The treadles were initially placed close together and near the food trough. Food was released into the latter before subjects were introduced to the arena. When the food already present had been consumed, the feeder was operated by the experimenter, and more food was dispensed. The experimenter continued to operate the feeder machine until the subject's behaviour indicated that it formed an association between the noise of the machine operating with the imminent presence of food. The criterion for this was the immediate interruption by the subject of whatever ongoing activity it pursued, by the operational sound of the feeder. When this stage was reached, the animal was considered to be ready to operate the treadles for a food reward by itself.

It was not necessary to employ procedures for shaping the operant responses, with the exception of one of the subjects. In general, the natural curiosity and levels of activity shown by the animals resulted in investigation of the operanda and contact with it.

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All subjects were given 18 minutes of magazine training per day and all subjects except one succeeded in developing operant responses within seven 18-minute training sessions.

During magazine training both treadles were presented without cardboard keys but the wooden bases of the former were visible through the Perspex lids. After magazine training the treadles were separated to a distance of 0.5 m and were maintained in a constant position in relation to the reward area, at a distance of 1.5 m.

Following the period of magazine training, test-sessions using serial reversals of discriminanda were initiated.

The experimental procedures employed in the principal tests were as follows:

Two subjects, E1 and E2, were tested on a series of spatial habit reversal tasks, using simple positional discrimination between right and left operanda. In these tests the position of the correct key remained constant, while the associated visual/tactile cues were randomly alternated according to a slightly modified Gellerman sequence.

Preliminary observations indicated a preference for the treadle slightly closer to the food and initial position-discriminations were counterbalanced accordingly to compensate for this factor.

Another two animals, E3 and E4, were tested on successive visual/tactile (black/rough surface and white/smooth surface) discrimination reversal problems. The treadles were arranged as in the previous experiment, a white cardboard key being inserted under the Perspex cover of one and a piece of black sandpaper being taped to that of the second. The animals were initially trained to operate the treadle with the white/smooth and black/rough keys respectively, and the positive (reward) stimuli were subsequently alternated throughout the experiment, the colour and texture of the correct keys being maintained constant between successive reversals but position was randomly alternated in accordance with a modified Gellerman sequence.

The general strategy of the investigation outlined above followed that described by Mackintosh *et al.* (1968).

The remaining two subjects, E5 and E6, were given a series of non-reversal shifts in which an animal initially trained on a spatial discrimination problem was subsequently given a visual discrimination problem, and *vice versa*. Initial discriminations were also counterbalanced in these tests, as described above.

A non-correction procedure was used in all experiments and continuous positive reinforcement was provided.

The reward consisted of small amounts of the normal dietary mixture supplied to echidnas and systematic food deprivation was used during the period of experimentation on each animal.

Ten trials per subject were provided in each daily experimental session for all subjects and the criterion was 20% or less errors in three consecutive blocks of 10 trials following a given reversal. When this criterion was reached, a new reversal was given. If a subject achieved criterion performance in the first block after a reversal, the experiment was terminated. Reversals were made at the commencement of daily sessions rather than between trials. Latencies (time in seconds) to initial and successive responses were recorded and scores of correct and incorrect responses were listed in order of occurrence, using standard protocol sheets.

After testing each subject, the apparatus within the room and the floor of the experimental room were cleaned with a dilute solution of detergent in an attempt to eliminate the use of odorous cues, as it has been suggested that echidnas may respond to secretions from the sebaceous glands of other echidnas (Dobroruka, 1960). The desirability of adopting such precautionary measures was also emphasised by Saunders *et al.* (1971a).

During the first 18 minutes of each daily session the subjects' activities were monitored by recording the frequencies of occurrence of several types of maintenance activities, as well as measures of the animals' rates of ambulation. The results of this aspect of the investigation forms the subject of a separate study.

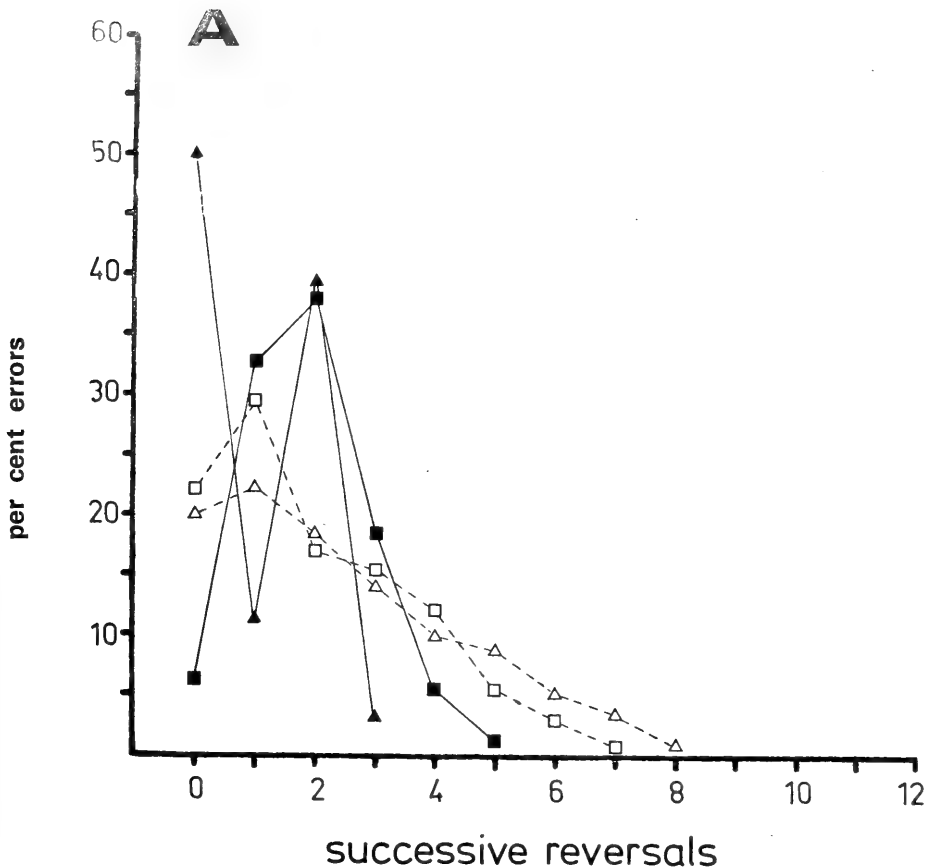
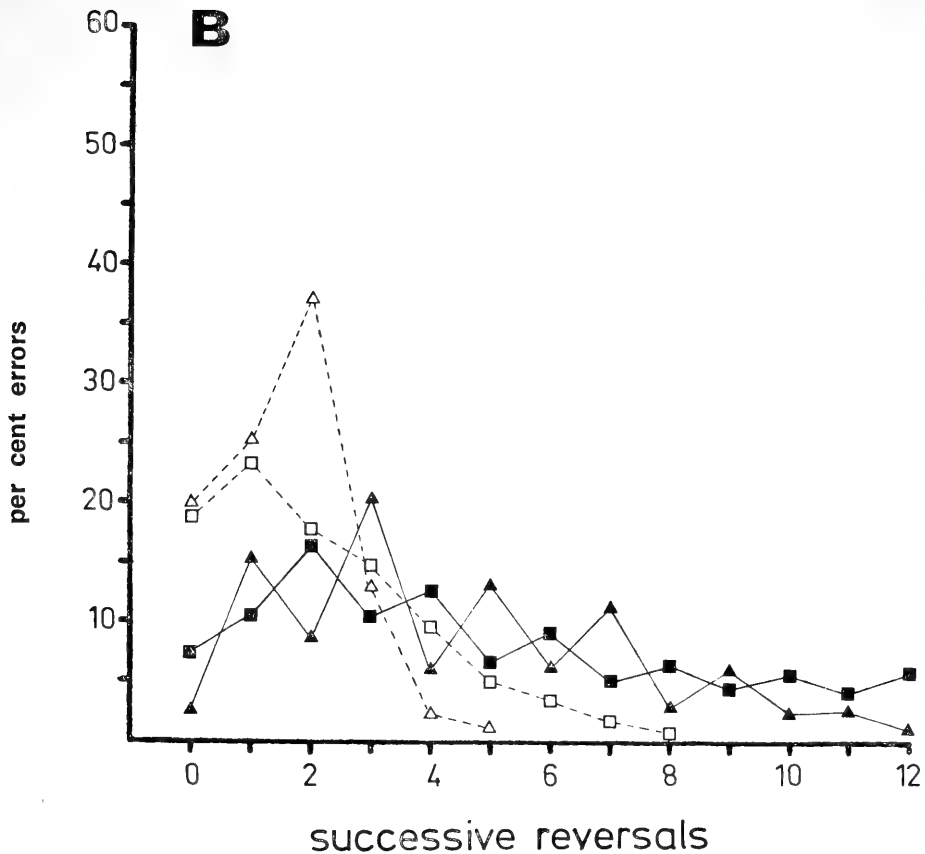


FIG. 2.—Changes in total errors (percentages) comparing: A. Positional reversal tests (Ss, E1 and E2; solid symbols) with visual/tactile reversal tests (E3 and E4; open symbols). B. Reversal shift tests (mean scores of positional reversals shown as open triangles; visual/tactile reversals as open squares) with non-reversal shift tests (Ss, E5 and E6; solid symbols). First point (0) represents the initial learning condition.

RESULTS

Echidnas introduced to the arena and operant apparatus exhibited several types of behaviour, including investigative (bill-sweeping, rearing, etc.) and ambulatory activities, as well as brief periods of immobility. These were monitored in an attempt to assess changes in motivation and emotionality, and also to relate levels of activity to the acquisition of learning, but are not considered to be immediately germane to the present study. However, it may be noted in passing, that the incidence of types of behaviour not directly associated with the manipu-



lation of the operanda and securing the reward gradually decreased over later trials, whereas operant and feeding responses increased, suggesting a selective concentration on the latter. The keys were invariably depressed with the forefeet, occasionally supplemented by the action of the hind limbs by walking over the treadles and unsuccessful (unrewarded) responses were often associated with vigorous kicking at the operanda.

All subjects were able to adjust to the test situations and responded to training. All of the echidnas succeeded in achieving criterion performance and all except one demonstrated learning-set formation. Response-latencies to operant activities, not considered in detail in the present study, generally decreased significantly over successive trials and often also within blocks of trials.

Figure 2a, illustrates changes in error-scores, based on percentages of all operant responses in successive reversals. These indicate that the subjects used

in positional reversal-tests were capable of superior performance to those tested in visual/tactile reversal shift conditions. Percentages of errors were high (but generally below 50%) in early trials and decreased consistently over successive reversals. The proportion of unsuccessful responses declined over each series of trials, but this was more rapid in tests using positional discrimination tasks. The number of reversals required to attain criterion-level of performance was also smaller in the latter; nevertheless, the subjects appeared to have improved in a remarkably short period in reversal shift tests using either type of stimulus situation. In non-reversal shift conditions the reduction in per cent errors was much less rapid and a correspondingly higher number of successive reversals was required to achieve criterion level—indeed, one subject (E6) failed to satisfy the criterion. Figure 2b is based on a comparison of per cent scores recorded in reversal shift tests and non-reversal shift conditions. These results indicate that performances in the latter are inferior and, in fact, the scores obtained in any single task of the reversal shift-type were, with the exception of the initial discriminations, better than those achieved in non-reversal shift tests.

Changes in the number of trials to criterion (not illustrated) were in general accordance with the foregoing observations. The number of trials required to attain the criterion was initially higher in visual/tactile than in positional reversal tests, and the number of reversals to criterion (7 and 8, compared with 3 and 5, respectively) also indicated that positional tasks are solved with greater facility. In non-reversal shift conditions, moderately high scores were obtained during initial testing, maximising in subsequent early reversals (blocks of trials) then decreased gradually. The single subject that satisfied the criterion required 12 reversals to do so.

The results illustrate that the learning curves obtained for *T. aculeatus* tested on instrumental discrimination tasks conform to the pattern generally yielded by eutherian mammals in comparable tasks. Furthermore, the course of individual performances also appears to be similar and suggest the use of a common essential strategy in the acquisition of learning. All but one of the subjects demonstrated negative transfer on the first reversal.

Reversal indices, *sensu* Munn (1964), were computed for the four subjects used in reversal shift tests, yielding scores of 2.75, 0.40, 1.00 and 1.06, with a mean value of 1.3.

This investigation was not specifically concerned with the role of memory in learning, but three subjects re-tested one month after the conclusion of the experiments achieved criterion level very rapidly, and one subject even exhibited one-trial reversal, suggesting a remarkable capacity for retention.

Figure 3 compares the performance of the subjects used in the present study with those of other species investigated in studies of reversal learning and is based on documented literature. *T. aculeatus* appears to compare favourably with other vertebrates, including eutherian mammals and the very rapid reduction of

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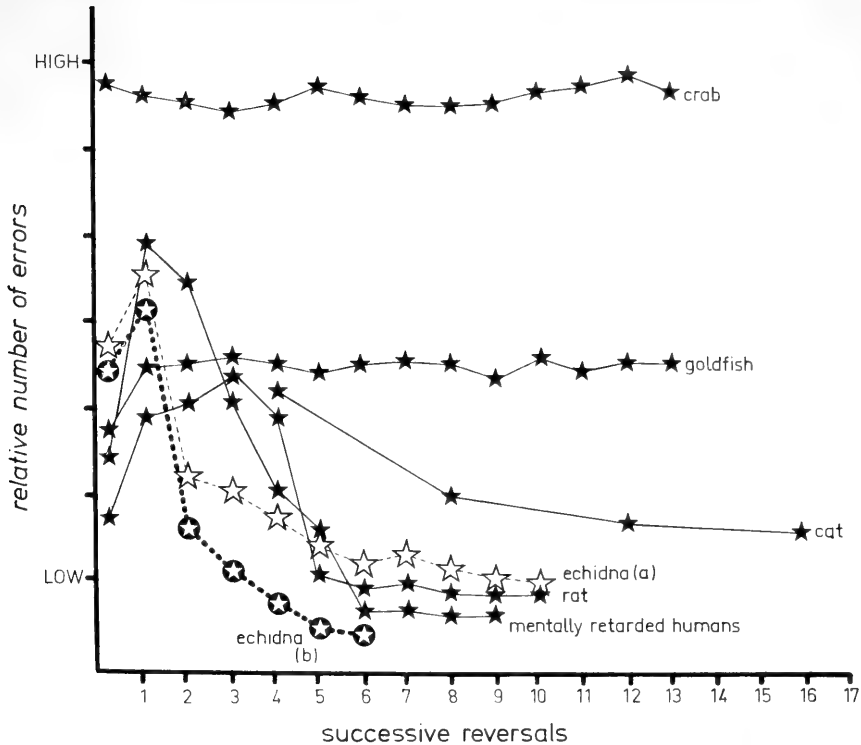


FIG. 3.—Comparison of the performance of *T. aculeatus* in tests of spatial discrimination-reversal learning with those of other animals, including: goldfish (Behrend *et al*, 1965), lab. rats (Dufort *et al*, 1954), cats (Cronholm *et al*, 1960) and mentally retarded human (House and Zeaman 1959). Echidna data is from two sources: (a) Saunders *et al*, 1971a, and (b) the studies reported in this paper.

errors exhibited by the subjects used in the present investigation, compared to those of Saunders *et al.* (1971 a,b) tested in a simple (and presumably less demanding) maze-situation, is noteworthy.

DISCUSSION

The present study probably represents the first documented investigation of instrumental reversal learning in a monotreme. The results indicate that echidnas are capable of performing successfully in tests of this type, particularly in tasks based on spatial discrimination.

Tasks involving visual discrimination-reversals are generally considered to be intrinsically more difficult than spatial (positional)-reversal problems. Furthermore, it is usually recognized that echidnas are not visually-oriented animals.

Although the brain of the echidna is fundamentally mammalian, several specific features of the organisation of the optical system are unlike those of eutherian mammals (Campbell & Hathow, 1971). There is no colour vision, cones being absent from the retina, but the presence of a pure rod retinal system, responsive to weak light stimuli, may be an adaptation to the shady or dark localities frequented by these animals, as in other mammals such as many insectivores and chiropterans. The absence of any effective mechanism of accommodation, as well as the small size of the optic chiasma and optic tract suggest that vision is poorly developed.

In view of the above considerations, visual and tactile cues were combined for the second type of discrimination problems used. Such a combination may be expected to yield a better performance than a series of discrimination tasks based exclusively on visual cues. The relative degree of utilisation of visual and tactile information was not determined in this investigation, consequently it is not possible to use the results of these tests for comparison with visual reversal-shift data obtained for other species. However, it is noteworthy that *T. aculeatus* is clearly capable of forming learning sets of tests other than positional (habit) reversals, particularly in view of the fact that several species have thus far proved capable of achieving this only in tasks of the latter type. Examples of such species include both invertebrates and vertebrates. Cephalopods (Mackintosh, 1962), fish (Wodinsky & Bitterman, 1957), pigeons (Reid, 1958) and even mammals such as kangaroos (Munn, 1964), proved successful only in positional reversal tests, although their failure to improve in task-situations using other types of cues may be due to other factors, probably including inappropriate methods of experimentation. Neumann (1961) reported that the performance of red kangaroos tested in a series of simple discrimination tasks compared favourably with house mice but were inferior to some other eutherians; other Australian marsupials appear to be capable of only moderate improvement in such tests (Munn, 1964; Buchmann & Grecian, 1974), but the North American opossum, *Didelphys virginiana* is surprisingly adept (James, 1960).

The individual performances of *T. aculeatus* tested in the present investigation were comparable to those of nocturnal rather than partly diurnal Australian marsupials used in previous studies, more trials being required to achieve reduction of errors in visual tasks to levels achieved in the final reversals of spatial discrimination tests. This did not appear to be due to persistent position habits as in some macropod marsupials (Munn, 1964; Buchmann & Jacob, unpublished data), although echidnas are capable of developing a position habit (Saunders *et al.*, 1971 b). The observed differences in performance may be a direct or indirect consequence of poor vision, as suggested by Buchmann & Grecian (1974), or may be explained by Seligman's (1970) concept of general "preparedness" to learn visual as opposed to spatial problems. Kirkby (1977) invoked this to explain the inferior performance of brush-tailed possum *Trichosurus vulpecula*, noting that the latter species is nocturnal and feeds on vegetable materials that do not

require active stalking or elaborate methods of hunting and manipulation of food. This may also apply with minor qualifications to echidnas, but the explanations proposed are not mutually exclusive and the disinclination of subjects to employ a poorly-developed sensory modality is hardly surprising. *T. aculeatus* probably uses spatial and olfactory, rather than visual, cues in foraging.

The paucity of studies on instrumental learning in non-eutherian mammals is a regrettable feature of the literature on comparative performances in learning. The few investigations available have concentrated exclusively on marsupials (James, 1955; Munn, 1964; Powell & Doolittle, 1971; Buchmann & Grecian, 1974), yet the present study demonstrates that at least one species of monotreme can be trained to manipulate simple operanda. The ability of this species to achieve instrumental "one-trial" learning (*sensu* Mackintosh *et al.*, 1968) also suggests that echidnas are capable of using the information supplied by some task-situations optimally (Dufort *et al.*, 1954; Cronholm *et al.*, 1960).

Further investigations are necessary to establish the reasons for inferior performance on visual tasks, but it is clear that echidnas are capable of consistent modification of their activities in tests using spatial (positional) discriminanda. Saunders *et al.* (1971a) reported systematic improvement both in terms of numbers of correct choices and of running times in their study of echidnas. A second investigation using spatial habit-reversal tasks showed that *T. aculeatus* is capable of attaining rapid improvement, including "one-trial" reversals (Saunders *et al.*, 1971b). The results of the present study confirm this and also indicate that echidnas can achieve considerable success in spatial-reversal tests employing operant rather than simple maze-techniques. In this respect, they are similar to those species of Australian marsupials that have received attention (Buchmann & Grecian, 1974), but not to the North American *Didelphis virginiana* (Friedman & Marshall, 1965). There is no evidence that the performance of echidnas is inferior to eutherian or metatherian mammals, and information on the extent to which they attend to spatial cues in naturalistic situations would be of considerable interest.

The results indicate that echidnas are able to improve in tests using reversal-shifts more easily than in non-reversal shift conditions. It is clear from the data that in both types of discrimination tests (positional and visual/tactile discrimination tasks), performances were superior in reversal-shift conditions. This type of selective improvement is generally regarded as evidence of some form of stimulus organisation or stimulus-coding, the animal storing, classifying and integrating the information it receives. In studies of learning in animals this phenomenon is often suggested to be an attentional process (Mackintosh, 1974) and may be considered to be a property of highly organised neural systems. It is evident from a comparison of reversal-shift and non-reversal-shift data that echidnas perform better in the former type of task, and this may indicate that they possess a complex level of cerebral organisation, if the concepts associated with this model of stimulus-coding are regarded as valid.

The subjects used in this investigation exhibited little evidence of improvement over early reversals, but a substantial reduction in errors occurred in later blocks of trials. This is similar to observations on other species of vertebrates tested in comparable situations (see Buchmann & Grecian, 1974); relatively poor performance during initial trials may indicate difficulty in relearning previously learned problems in the absence of appropriate experience.

Saunders *et al.* (1971a) noted that the acquisition of a position habit by *T. aculeatus* is similar to the corresponding process in laboratory rats in T-mazes, given approximately the same amount of training and improvements in the running speeds of echidnas, are comparable to those of rats in runway-situations. Saunders *et al.* subsequently (1971b) demonstrated rapid improvement by echidnas tested on serial position-habit reversal tasks and reported that their performance was essentially more similar to those of mammals than other vertebrates. These conclusions were based on the small number of reversals required to achieve significant reduction in error scores and the frequent occurrence of one-trial reversals, these being characteristic features of the learning process of mammals (Dufort *et al.*, 1954; Mackintosh *et al.*, 1968), but not of species belonging to other vertebrate classes.

The reversal indices obtained in this study compare favourably with values reported for several marsupial and eutherian species (Munn, 1964). However, the usefulness of such derived indices is questionable (Buchmann & Grecian, 1974) and the general strategy employed in the acquisition of learning is probably more important.

Saunders *et al.* (1971b) suggested that detailed comparisons of the learning performances of monotremes with those of eutherian mammals would be of considerable interest and importance. The results obtained in the present investigation compare favourably with such mammalian species as cats (Cronholm *et al.*, 1960), rats (Dufort *et al.*, 1954) and human mental retardates (House and Zeaman, 1959). These studies, as well as the present investigation, were based on training subjects to a criterion level over successive reversals, but the performance of the echidnas used in this study also appeared to be superior to those of Saunders (1971a), who employed a fixed trials procedure, with reversals given regardless of previous performance. *T. aculeatus setosus* is clearly capable of criterion performance in a smaller number of reversals than other mammals tested on instrumental tasks. However, the shape of the learning curves obtained may be more important than the speed of attaining a criterion. The latter may be influenced by the method of testing employed (simple operant techniques rather than the W.G.T.A. type experimental designs used in most comparable studies). The shape of the learning curves obtained in the present investigation are unmistakably of the characteristic mammalian type.

The mammal-like performance of echidnas in tests of learning ability is not surprising in view of their cerebral anatomy. Compared with those of reptiles

and birds, the principal features of the brain of *T. aculeatus* suggest that these monotremes have greater affinities to eutherians than to other vertebrates. The cerebellum is conspicuously enlarged and divided into a number of lobes whose surfaces are thrown into folds. This results in a substantial increase in the quantity of superficial grey matter in the cerebellar cortex. The most conspicuous feature of the telencephalon and, indeed, of the brain viewed in its entirety, is the pronounced development of the cerebral cortex. The brains of monotremes, like those of most marsupials, are devoid of the corpus callosum, but the dorsal hippocampal commissure which connects the lateral hippocampal areas in reptiles is present. Although the neo-cortex is generally well developed in mammals, the large cerebral hemispheres of *Tachyglossus* and *Zaglossus* have been a source of interest, even of astonishment, to many neuro-anatomists. Elliot Smith (cited by Griffiths, 1968) wrote in 1902, "The most obtrusive feature of this brain is the relatively enormous development of the cerebral hemispheres, which are much larger both actually and relatively than those of the platypus. In addition, the extent of the cortex is very considerably increased by numerous deep sulci. The meaning of this neopallium is quite incomprehensible. The factors which the study of other mammalian brains has shown to be the determinants of the extent of the cortex fail completely to explain how it is that a small animal of the lowliest status in the mammalian series comes to possess this large cortical apparatus." More recent investigators, notably Allison & Goff (1972), also commented on the large size of the brain and concluded, on the basis of electro-physiological studies, that the neural organisation of echidnas is fundamentally similar to eutherian mammals. Current studies (Dr. L. Neylon, *pers. comm.*) are directed at establishing the function of the highly enlarged frontal lobes, these structural features being generally associated with complex cerebral processes such as intelligence, memory, insight and voluntary behaviour (Teitelbaum, 1967). The size of the brain viewed *in toto* may also be important. Warden (1951) suggested that the ratio of brain-mass to spinal cord-mass is a useful index of neural organisation and intelligence, based on the following examples of representative ratios: in fish the mass of the brain is less than that of the spinal cord, in the cat the ratio is 4:1, in a monkey it is 8:1 and in man 50:1. Neylon (*pers. comm.*) estimated the corresponding ratio for *T. aculeatus* at 6:1. The anatomical features described above are clearly compatible with the view that echidnas should be capable of learning tasks of at least moderate complexity despite their generally accepted taxonomic position. Further studies are required on the acquisition of information and memory to resolve the apparent conflict between the currently-available anatomical and behavioural evidence and the lowly status generally assigned to this species among mammals.

It would be tendentious and sanguine to claim that echidnas are superior to other species of animals tested in comparable learning situations, but the results obtained in this study cast doubts on the validity of several investigations of this type. "Contamination" by motivational or emotional factors and generally inappropriate methods of testing and assessment may influence the results of such

studies. Provided that stringent efforts are made to minimize experimental trauma, provide suitable incentive to learning, and pose problems that are designed as tests of adaptive behavioural changes rather than of specific sensory modalities and/or motor skills, echidnas are good potential subjects for studies of instrumental conditioning. Further studies of learning will undoubtedly disclose important facts about the intelligence of these remarkable animals and modify the quaint, explicitly or tacitly-held views that echidnas are little more than animated pin-cushions or, at the best, glorified reptiles.

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Vision in the Monotreme Echidna (*Tachyglossus aculeatus*)

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ABSTRACT

Echidnas were trained in simultaneous, two-choice, visual discrimination tasks to distinguish between black and white stimuli and between vertical and horizontal stripes of varying widths. In a second set of behavioural experiments interocular transfer of visual information was examined for stimuli of varying complexity. In spite of the acallosal nature of the echidna, high levels of visual transfer were shown.

Retinoscopic examination of the eye of *Tachyglossus aculeatus* revealed that it is capable of accommodation even though intraocular muscles are apparently absent.

The data from this study suggest that the echidna has visual capacity which is better than previous observers would have had one believe.

INTRODUCTION

The visual system of the echidna is an unusual mixture of both reptilian and mammalian characteristics (Griffiths, 1968). For example, the sclera of the eye contains a cartilaginous cup which is characteristic of the sauropsidan eye, while the arrangement of its extrinsic eye muscles is like that of so-called "higher" mammals (Griffiths, 1968). The absence of any apparent mechanism of accommodation, coupled with the relatively small size of the visual tract, has led most observers of the monotreme visual system to conclude that eyesight is probably not one of this animal's strong points. Some authors (see for example Allison *et al.*, 1972, p. 173) have even gone so far as to draw a comparison between the vision of echidnas and that of other visually "poor" species, such as the "virtually blind" mole and the bat.

However, at least one author (O'Day, 1952) has suggested that sight of echidnas may not be as defective as one is led to believe from their apparently poorly-developed visual anatomy.

In the absence of any empirical work on the visual behaviour of the echidna it is difficult to draw any conclusion about their visual capability. The following

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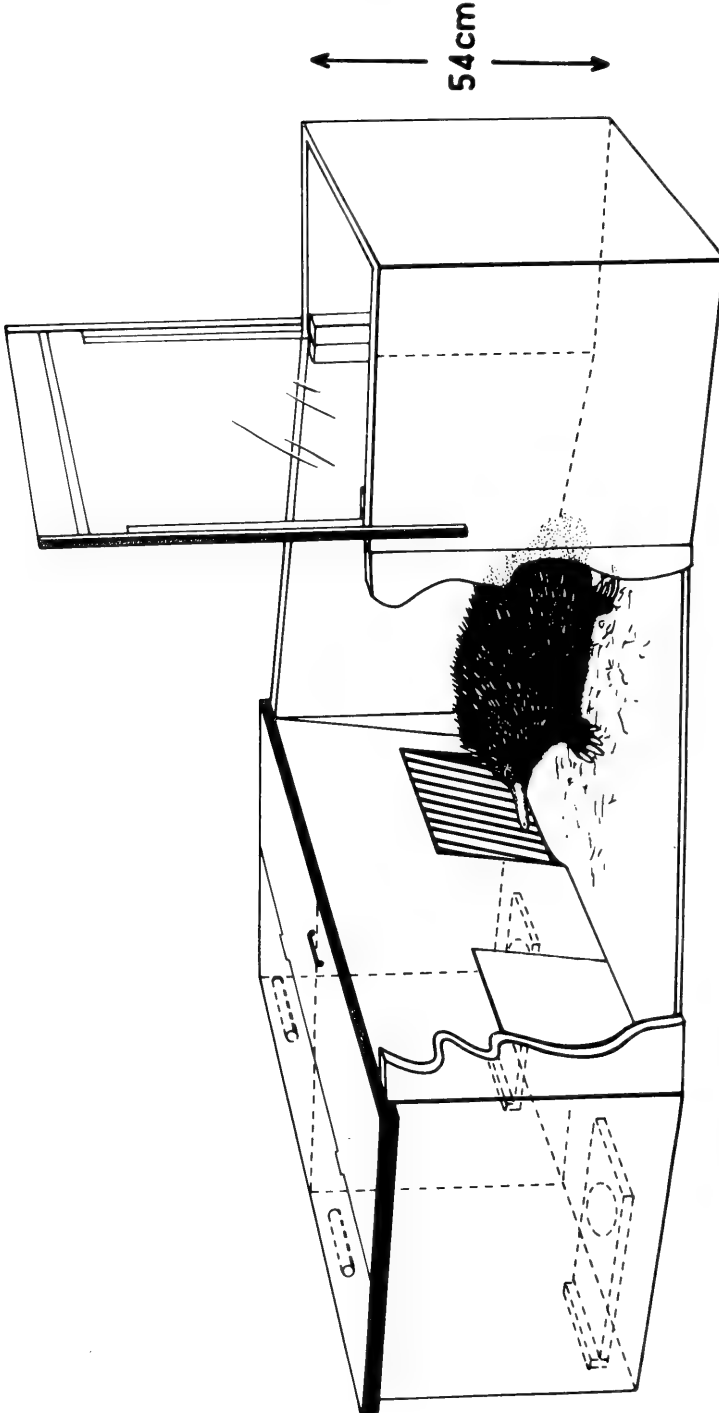


FIG. 1—The discrimination apparatus with an echidna pushing open the stimulus panel door to one of the goal boxes. Also shown are the manually-operated food magazines and fluorescent lights inside each goal box. Overall box length is 195 cm.

series of experiments were designed to examine some aspects of visual behaviour and function in the echidna, *Tachyglossus aculeatus*.

SIMPLE VISUAL DISCRIMINATIONS

Saunders *et al.* (1971a, 1971b) have previously shown that echidnas can learn a position habit and a position habit reversal, but there are apparently no reports that echidnas can learn to make visual discriminations. The first series of experiments were, therefore, designed to determine if echidnas could learn simple visual discriminations.

MATERIALS AND METHODS

MAINTENANCE OF ANIMALS

All echidnas were maintained in a large, wooden box 60 cm wide by 300 cm long by 67 cm deep. The galvanized iron tray bottom of the box was covered with three to four inches of sawdust and wood shavings, and was kept in one room of an air-conditioned animal house. The animals were maintained on a cycle of 12 hours light and 12 hours dark; room temperatures varied from a minimum of 20.6°C to a maximum of 22.8°C. Until the time of food deprivation for each experiment the animals were maintained on an *ad libitum* soup-like diet consisting of raw egg, meat and bone meal, pollard, glucose, water and Pentavite.

Following some initial problems with diet and maintenance of optimum animal health, oleic acid and Nutrivet (Nicholas Pty. Ltd.) were added to the diet, and an infra-red heat lamp was mounted at one end of the house box.

DISCRIMINATION APPARATUS

Figure 1 shows a three-dimensional drawing of the discrimination apparatus used in all the visual discrimination experiments reported here. Minor modifications, such as wall colour, backlighting and central divider, were made to the unit as experiments progressed, and as the need for refinements and improvements arose.

Basically, the discrimination box, built from half-inch chipboard, consisted of a start box, runway and two goal boxes. The inside walls were painted a flat, medium grey.

A door frame was attached to the top of the entrance of each goal box by hinges. By putting pressure on the frame, the door could be opened from the bottom. The door could not be pushed open from inside the goal box, as the entrance walls to the goal box prevented outward movement. Guide rails attached to the back of each frame permitted the stimulus panels (26 x 26 mm) to be removed and reinserted, thus filling in the gap in the frame. In later experiments the door arrangement was modified so that a sandwich panel could be fitted into the guide rails, and even later so that the stimulus panels could be hung from the top of the door behind a thin, transparent plexiglass door, thus removing the stimulus panel from direct contact with the animal.

Food reinforcement was obtained by the echidna from a food tray in the floor of each goal box. The tray was mounted in a sliding wooden drawer which could be manually withdrawn. Partial withdrawal of the food drawer occluded the feeding access hole, preventing the animal from obtaining food.

Vertical guide bars mounted on the sides near the back of each goal box served as guides for removable, secondary stimulus panels. These panels were made from plexiglass and occupied the whole rear surface of each goal box.

The floor of the discrimination apparatus, except for the goal boxes, was covered with sawdust to absorb echidna scats. The animal was prevented from leaving the start box by a guillotine door, which was raised manually at the beginning of each trial. Once the echidna had made a discrimination choice and had entered the goal box, the door automatically fell shut, trapping the echidna in the goal box.

The discrimination apparatus was placed in the centre of an air-conditioned room, which was fitted with overhead fluorescent lamps mounted behind diffusers. This light provided an ambient light level for the discrimination apparatus in the human photopic range.

EXPERIMENT 1: BLACK-WHITE DISCRIMINATION

The first experiment was designed to see if echidnas could learn a simple visual discrimination.

MATERIALS AND METHODS

(a) *Experimental Animals*

Three echidnas, E1, E2 and E3, of unknown age, weighing between 1.27 and 1.87 kg, were used. All three had been captured from the bush around Melbourne at least three weeks prior to experimentation. The animals had been fed *ad lib* prior to the beginning of the experiment.

(b) *Pre-experimental Handling*

All echidnas captured from the wild took some time to adapt to their new surroundings. Before an animal was used as a subject it was handled for at least one half hour daily, until it seemed to be adapted to its new environment and to the handler. Echidnas were fed only during this half-hour period.

For all animals, regardless of previous experience, one week of handling for one half hour per day was given before experimental training began.

(c) *Stimulus Panels*

Stimulus panels were made from black and white plexiglas; the black panel was opaque and the white panel translucent. No back lighting was used; the apparatus was illuminated with ordinary overhead lighting as described earlier.

(d) *Familiarization Training*

At the end of the week of daily handling, and at approximately the same time every day ($\pm \frac{1}{2}$ hour), each food-deprived echidna was taken to the discrimination apparatus and placed in the start box, with the start box and goal box doors open; the echidna was left to explore the discrimination apparatus. The animals soon learned to move down the runway to the goal boxes and food. Each animal then had one daily (20 trial) session of familiarization training for six days. For the first 30 trials the guillotine door was opened and closed for each trial, but the goal box doors were kept open. For the remaining 90 trials the goal box doors were closed, and the animal had to learn to push them open. This took approximately two to four trials to accomplish. Each trial was rewarded with a 30-second feed in the goal box. Each animal was given a 60-second rest in the start box between trials. Preferences for the black or white stimulus panels were noted.

(e) *Experimental Condition*

On completion of familiarization training, the three echidnas were given six daily sessions of 18 correct trials, for a total of 108 trials; that is, each echidna had to choose the correct panel 18 times on any one session for six consecutive sessions. The number of trials was reduced to 18 because performance of the animals, in terms of speed of making a choice, dropped considerably in the last one or two trials in training. For a correct choice, the animal was rewarded with a 30-second access to the food; for an incorrect choice, the food was withdrawn, and the echidna was left in the goal box for 15 seconds before being returned to the start box for a new trial. Incorrect choices were counted as errors. The food magazine was withdrawn only after the animal made an incorrect choice and was inside the goal box . . . but before it had reached the food. This procedure was followed to control for olfactory cues that might have led the animal to make its discrimination on the presence or absence of the smell of the food emanating from the open food tray. Additional olfactory cues that might have come from the stimulus panels, because of repeated contact with the beak of the echidna, were also controlled for by wiping clean both panels at each intertrial interval.

To control for position habit, the stimulus panels were alternated between the left and right goal box doors according to a two-choice position series developed by Fellows (1967).

ECHIDNA VISION

Two of the main features of the series are (1) that one particular stimulus panel was never on one side for more than three consecutive trials, and (2) that the positive stimulus appears equally often on the left or right sides on each daily session. Regardless of whether a panel had to be moved from one side to the other or not, the panels were removed and replaced for each trial to control for auditory cues. Secondary black and white cue panels at the back of each goal box were also moved back and forth between the left and right sides with the other panel from the door to the goal box. Secondary stimulus panels were included, so that animals had an opportunity to observe the negative stimulus panels while in the goal box.

In the training session, E2 chose the black panel more than 12 times out of 20 and was thus trained to approach the white panel. E1 and E3 were reinforced in the experimental condition for approaching the black panel. At the end of each 18 correct trial session, all animals were given a five-minute supplementary feed.

RESULTS

The performance of the three animals on each of the six experimental sessions is shown in Figure 2A. The significant improvement in performance between the first two sessions and the last two sessions is self-evident (correlated $t = 4.55$, d.f. = 2, $P < 0.05$, two-tailed).

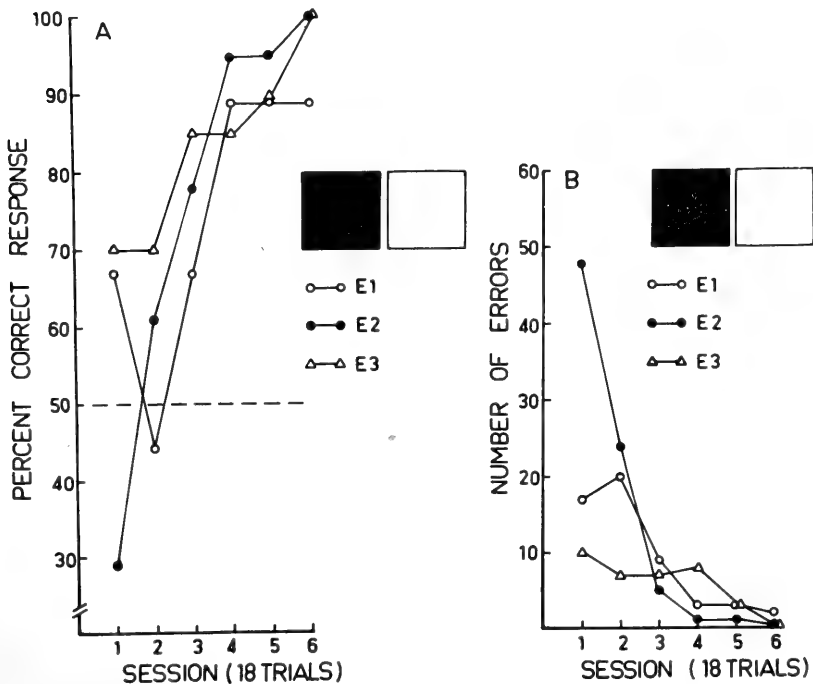


FIG. 2—A. Individual performance curves during acquisition of the black-white visual discrimination in three echidnas. B. Individual error-rate curves during acquisition of the black-white task. Note the rapid decrease in error-rates for all three echidnas from session 1 to session 6.

As the individual curves show, all three animals very quickly learned to discriminate between black and white. By session six, E2 and E3 were choosing their respective correct stimuli 100% of the time, and E1 had reached the 89% correct response level. Figure 2B demonstrates the rapid reduction in error rate which occurred from sessions one to six for all three echidnas.

DISCUSSION

The data from this experiment confirm that the echidna is capable of making a brightness discrimination under photopic lighting conditions. The experiment also indicated that the echidna is quite a tractable animal in this type of simultaneous visual discrimination task. The performance would appear to be under stimulus control.

EXPERIMENT 2: VERTICAL-HORIZONTAL DISCRIMINATION

The second visual discrimination task given to the echidnas was the more complex vertical-horizontal discrimination (Lashley, 1930).

MATERIALS AND METHODS

(a) *Animals*

Five male echidnas, ranging in weight from 1.27 to 2.25 kg, were used in this task. All had had previous experience on the black-white task. E4 and E5 had been used in an initial black-white pilot study and had also learned the discrimination.

(b) *Discrimination Apparatus*

The testing apparatus was the same as that used in Experiment 1, except that a system of back lighting was used for the stimulus panels. This system consisted of two 13 cm fluorescent tubes (Philips TL W4/33), one mounted on the ceiling of each goal box. The lighting level in each goal box was well above the human upper scotopic limit of level of illumination. The experimental room was kept in darkness throughout the experiment.

(c) *Stimulus Panels*

The stimulus panels were made from translucent white plexiglas. Black lines were painted on one panel in a horizontal orientation and on the other in a vertical orientation. When hung on the door frame, the back lighting effectively lit up the panels, and the vertical-horizontal lines were clearly illuminated. The panels were matched for luminance (11 candelas/m^2), measurements being made with a Macbeth illuminometer (model 6800).

Five different widths of stripes were used in this experiment. The first discrimination employed 25.4 mm stripes. Conditions two through five were lines of steadily diminishing widths: 12.7 mm, 6.35 mm, 3.18 mm and 1.59 mm respectively. With the two smallest widths of stripes, the stimuli were put behind a thin sheet of clear plexiglas so that the echidnas could not interfere with the tape that was used to make up the stripes of the last two stimuli. This technique also acted as an effective control against discriminations that might have been based on tactile information gained by running the nose across the stimulus panel. This new technique of stimulus presentation also obviated the need to wipe the panels clean between each trial to control for olfactory cues. The clear front plexiglas panels were now permanently hinged to the goal box entrance. Only the back stimulus panels were moved from trial to trial.

(d) *Procedure*

As all animals had previously been handled, no familiarization training session was instituted for this experiment. The animals were maintained on a deprivation schedule which allowed them to feed only in the experimental situation. No food was available in the home box.

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The animals were run using the same procedure as that employed for the black-white discrimination, except that access time to food reinforcement in the goal box was limited to 20 seconds instead of 30 seconds, and supplementary feeding time was reduced from five minutes to two minutes. This decrease in feeding time was instituted to ensure that the animals were kept hungry and therefore in a "well-motivated" state.

On the day before discrimination training began, all animals were tested for a preference for either vertical or horizontal lines. The preference test consisted of letting the animals make 20 non-reinforced choices of the 25.4 mm stimulus panels in the discrimination box. If the animal chose one panel more often than 12 times out of 20, then the non-preferred panel was chosen as the positive stimulus panel for experimental reinforcement. If an animal showed no preference, then it was randomly assigned to either one of the two stimuli. If an animal was assigned to horizontal stripes at the beginning of the experiment, then it was reinforced for a horizontal choice for the remaining set of line widths. In this experiment three animals were reinforced for horizontal stripes and two for vertical stripes.

In discrimination training, each echidna was reinforced for 20 correct trials per session for each set of line widths. A record was kept of the number of correct trials per session. For each of the 25.4 mm and 12.7 mm line widths, six sessions of reinforcement performance were run. For conditions 6.35 mm, 3.18 mm and 1.59 mm, two, four and five sessions were run respectively. The number of sessions was reduced for each of the conditions because a number of animals began to lose condition. When it became apparent that a high level (better than 85%) of mean group performance had been reached for each line width, then the five animals were moved to the next and smaller width condition. At the end of the 1.59 mm width condition, four of the five animals were returned to *ad lib* feed, as they appeared to be thin and not in good condition. One animal was continued on a 1 mm task and a record of its performance noted.

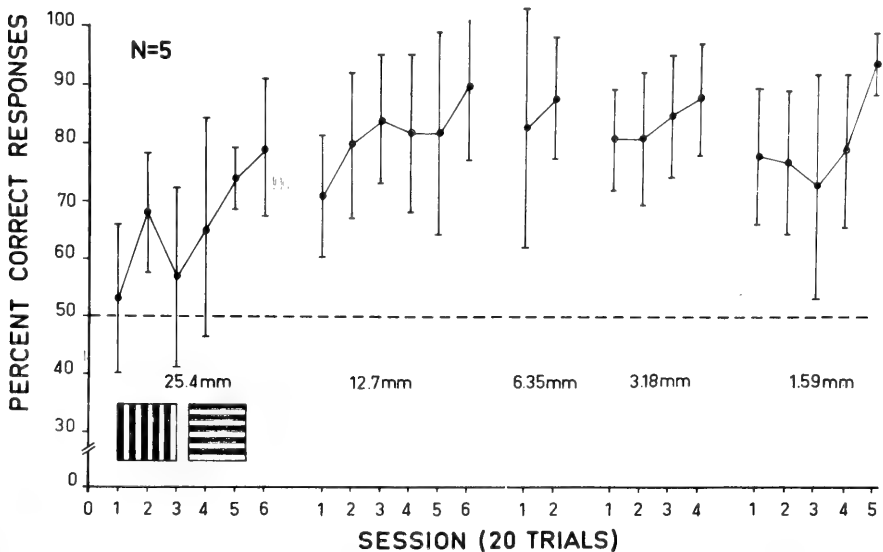


FIG. 3—Mean performance curve for five echidnas during acquisition of the vertical-horizontal visual discrimination and for transfer training for the same task with stripes of diminishing widths. Vertical bars represent \pm one S.D. Stripe widths are given in mm below the respective sessions.

RESULTS

The mean performance for five echidnas for each session is shown in Figure 3. A statistical comparison between the performance of the echidnas on session one and session six of the 25.4 mm width lines shows that there is a significant difference in performance (correlated $t = 10.61$, d.f. = 4, $P < 0.001$, two-tailed), indicating that learning has taken place and that, therefore, echidnas are capable of making a discrimination between vertical and horizontal stripes.

A comparison between the performance of the animals on session six of the 25.4 mm stripes and session one of the next condition, the 12.7 mm stripes, shows that although there is a slight drop-off in mean performance from 79% correct to 71%, the change is not significant statistically (correlated $t = 1.55$, d.f. = 4, $P > 0.2$ two-tailed). These findings indicate that there is transfer of learning from one width of stripes to the next and smaller width of stripes. A comparison between session one and six of the same width condition reveals that performance further improved in the course of the six sessions (correlated $t = 10.16$, d.f. = 4, $P < 0.001$ two-tailed). Comparison between the last session of any one condition and the first session of the next consecutive smaller stripe width indicates that performance and, therefore, transfer of training were maintained.

DISCUSSION

From the results obtained it is apparent that echidnas can learn to discriminate between vertical and horizontal stripes with relative ease. Moreover, this ability to be able to discriminate implies that the echidnas are capable of making a distinction between information differing in orientation (Sutherland, 1961). The continued maintenance of the discrimination over a reasonable range of stripe widths also suggests that the animals are capable of visual stimulus transfer.

The maintenance of the discrimination over conditions strongly suggests that this task could be a useful technique for examining visual acuity in echidna. Although this particular experiment lacks a physical choice point at which to force the animals to make a discrimination (distance at which a choice is made from the stripes being critical for calculation of acuity), note was made of the point at which the animals appeared to be making their decision. For some animals this could be determined fairly easily. For example, an animal would leave the start box and run down the runway toward an incorrect stimulus panel and then would abruptly change direction and go to the correct panel. The point where this abrupt change occurred was labelled the "choice" point. It must be kept in mind, however, that it was only a rough approximation of distance at which discrimination was occurring. In three of the animals this point was a minimum of 20 cm from the nearest stimulus panel. The tracks the echidnas left in the sawdust on the bottom of the runway acted as a record which, after correcting for distance between head (eye) and feet of the echidna, gave a rough idea of where the discrimination had been made. Assuming a 20 cm distance for the 1.59 mm lines, the angle subtended for a single point at the eye for 1.59 mm

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lines would be approximately 0.455 degrees. In comparison with the rat's performance on a similar task, the echidna is at least as good as the hooded rat and better than the albino rat. For hooded rats a discrimination of this type breaks down at 1.5 mm. Under the conditions of Lashley's (1930) test, the threshold of the pigmented rat for stripes was below 52' of arc and above 26'.

The one echidna which was run on the 1 mm stripes was also consistently able to maintain its discrimination, and there was no sign of a breakdown in performance. On the first session of the 1 mm discrimination task, the animal scored 85% correct responses.

These two discrimination experiments are valuable in a number of respects. First of all, they show on an experimental basis that echidnas are capable of learning to make visual discriminations. Second, these experiments establish that echidnas can make a brightness discrimination, and discriminations between stimuli differing in orientation. In addition, the series of vertical-horizontal discriminations establishes that echidnas have the capability for making discriminations which demand visual acuity. Although inconclusive, the experiments suggest that echidnas have visual acuity capability which is probably equivalent to that of the hooded rat. The most important point to be drawn from this discrimination work is that echidna vision does not appear to be as dismal as some of the anatomists would have one believe (see for example Prince, 1956, p. 163).

INTEROCULAR TRANSFER

Much previous work in so-called "higher" mammals has implicated the corpus callosum in transfer of visual information from one eye to the other (Levinson and Sheridan, 1969). Bianki and Morozova (1964) have each gone as far as to suggest that the corpus callosum is not only a pathway to convey visual information between hemispheres, but that it is essential for analysis of visual shapes, at least for the "lower" mammals. As monotremes and some marsupials lack the corpus callosum, there is some considerable interest in transfer of visual information between cerebral hemispheres for these mammals. Because the echidna also has almost total decussation (crossover) of optic nerve fibres (Campbell and Hayhow, 1971) this monotreme would seem to be the ideal "natural" split brain preparation for the study of interocular transfer of information.

The following experiments were designed to explore interocular transfer in the echidna.

METHOD AND MATERIALS

PROCEDURE

A series of two choice, simultaneous discriminations were employed for the interocular transfer experiments reported here. Animals were trained to approach one of two visual panels for a food reward. A standard training and testing procedure, slightly modified from that of the previous experiments, was used for all three interocular transfer tasks. Several days prior to training, the animals were food deprived and fed only during a half-hour daily

handling session until their characteristic defence postures had disappeared. When manageable, they were trained for two days (20 trials each day) to run down the alleyway of the discrimination box and push open a door to obtain food reward in the goal box. The discrimination procedure was then introduced and consisted of training animals with one eye occluded to open the door of the correct stimulus panel for a food reward. Both goal boxes were baited on each trial to control for solution by olfactory cues, and the incorrect box was always locked shut to prevent the animal from entering. An error was recorded whenever the animal pushed or touched the incorrect door. The trial, however, was continued until a correct choice was made, and the echidna was allowed 15 sec. to feed in the goal box. At the end of each daily 20-trial session all animals were given a two-minute supplementary feed.

The position of the correct stimulus panel was changed from trial to trial, as in the previous discrimination experiments (Fellows, 1967) to control for the possibility of solution of the visual discrimination by position habit. Training was continued until the echidna met a criterion performance. To test for interocular transfer, the occluding patch was changed to the opposite eye on the next test session and the training continued with the naive eye until the same criterion was met.

At the end of transfer training both eyes were occluded and the animals run on the discrimination without vision. Chance performances confirmed that discriminative response was under visual modality control and that the patches were effectively occluding the eye.

EYE OCCLUSION

The eye was occluded with a patch made from 5 cm elastic sticking plaster covered with opaque, black, plastic tape. Each animal was lightly anaesthetized with fluothane and the heavy facial hair shaved off in the region of the eye to facilitate application of the tape occluder over the eye and a wide area of the surrounding skin. This procedure was repeated every day, so that the eye patch could be effectively applied. Following occlusion, the animals were allowed to recover for about an hour before testing began. Anaesthesia was discontinued for the second and third experiments.

DISCRIMINATION APPARATUS

The apparatus used for the interocular transfer experiments was slightly modified from that used in experiments one and two. A 20 cm by 12.7 cm board was attached to the wall of the goal box and floor of the runway at the centre point between the two goal boxes. This board acted as a divider between the two goal box doors. The goal box doors were also modified: a square of (3.75 mm thick) clear plexiglas replaced the previous doors of the goal boxes. On the back and top corners of each door small diameter, 15 mm screws were driven at right angles into the plexiglas surface; these screws were then used to hold the stimulus panels on the back of the clear plexiglas doors.

EXPERIMENT 3: INTEROCULAR TRANSFER OF A BLACK-WHITE DISCRIMINATION

A number of Eutherian mammals with corpus callosum intact or sectioned, and with a very small number of ipsilateral optic fibres intact, have shown interocular transfer of a black-white discrimination (see for example Sheridan, 1965, and Lynch and Sheridan, 1970).

The following experiment was designed to examine interocular transfer of a black-white brightness discrimination in the "naturally" acallosal echidna.

METHOD

(a) *Apparatus: Stimulus Panels*
As for experiment one.

(b) *Experimental Animals*

Four healthy, naive echidnas of unknown age, weighing between 1.85 kg and 3.76 kg, were used for this experiment. Two animals came from the Canberra area, and the other

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two came from South Gippsland in Victoria. All four animals had been taken from the wild at least two weeks prior to the beginning of familiarization training, and had been carefully examined for external parasites before admission to the animal holding quarters.

Of the four animals used in this experiment, two were reinforced for choosing the black panel and two for choosing the white panel. For both the black and white panels one animal was trained with the left eye first, and the other with the right eye first.

RESULTS

Figure 4 shows per cent correct response for each echidna for each session on both initial and transfer discrimination training. All four echidnas reached criterion on the first eye within 100 trials, and criterion on the second eye within 40 trials, a saving of approximately 60 trials.

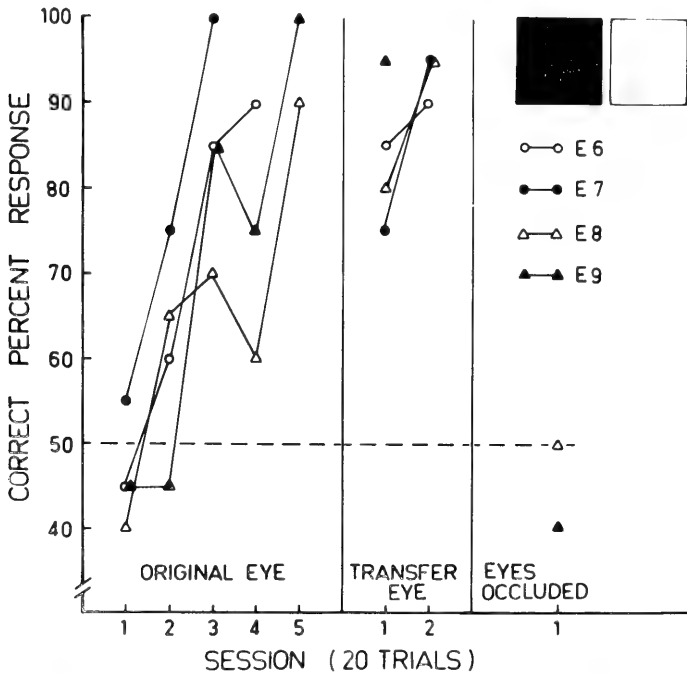


FIG. 4—The left side of the fig. shows acquisition of a black-white discrimination to a criterion of 90% correct for four echidnas with one eye occluded. The middle section shows acquisition of the same discrimination for the same animals with the trained eye occluded and the naive, transfer eye uncovered. Results on the right side of the fig. are for E8 and E9 with eyes occluded.

From the last day's performance for the first-trained eye, to the first day of transfer training for the naive eye, there was a drop in performance; however, this change was not significant (correlated $t = 2.38$, d.f. = 3, $P > 0.05$, two-tailed). The results indicate that transfer of training had taken place. Moreover,

a comparison between the first day of training for the first eye and the first day's performance for the naive transfer eye showed that the change in performance was significantly different (correlated $t = 5.96$, d.f. = 3, $P < 0.01$, two-tailed), further indicating that transfer had occurred.

DISCUSSION

The results of this experiment show that there is a transfer of training between eyes for a black-white brightness discrimination task. The transfer eye does not appear to have to completely relearn the black-white discrimination. One echidna, E9, reached criterion on the first day of transfer, and the other three animals reached criterion on the second day of transfer. This decrease in number of trials to criterion would indicate considerable "savings" from the previously-trained eye, which required from three to five days to reach the criterion.

Similar transfer of training has been shown for pigmented rats which have undergone corpus callosum section, but which have both ipsilateral and contralateral optic fibres intact (Sheridan, 1965). However, similar transfer has not been shown for albino rats with the same callosum sectioning. Differences in number of ipsilateral fibres between albino and pigmented rats may be the critical factor here (Sheridan, 1965; Lund, 1965). There are a number of similarities between the callosum-sectioned pigmented rat and the intact echidna, which might explain how transfer is occurring in the echidna: both are acallosal and, therefore, must be using some other method to achieve transfer; both have a small number of uncrossed optic fibres and an anterior commissure which could be used either separately or in combination to achieve transfer.

EXPERIMENT 4: INTEROCULAR TRANSFER OF A VERTICAL-HORIZONTAL DISCRIMINATION

Schneider (1969) has demonstrated that surgically-acallosal hamsters are capable of monocular acquisition and interocular transfer of a vertical-horizontal discrimination, indicating that for hamsters at least the corpus callosum is not essential for transfer of training of visual orientation information. Moreover, Levinson (1972) has shown substantial interocular transfer of orientation information in acallosal guinea pigs which are estimated (Polyak, 1957) to have 99% decussation of the visual fibres (similar to echidna). The following experiment was designed to examine interocular transfer of a monocularly-acquired, vertical-horizontal discrimination in echidna.

METHOD

(a) *Experimental Animals*

Three animals, E6, E7 and E9, were used in this experiment. All had taken part in the black-white interocular transfer task and were therefore familiar with the discrimination box and handling. The animals had been returned to *ad lib* feed for two weeks prior to the beginning of this experiment.

(b) *Feeding and Familiarization Training*

For one week each echidna was fed and handled on a daily basis for half an hour. At the end of this week the animals were taken to the discrimination apparatus and trained

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as described in the previous experiment until 20 trials per day for two consecutive days had been reached. On completion of familiarization training, discrimination training commenced the next day.

(c) Stimulus Panels

As for the 25.4 mm task of experiment two.

RESULTS

Figure 5 shows per cent correct responses for each animal for each session of discrimination training for both original and transfer eyes. As the per cent correct response curves show, E6, E7 and E9 learned to criterion with the first eye in six, seven and six days respectively. However, learning to criterion with the second eye took considerably less time, with E6, E7 and E9 requiring only two, two and three days, respectively, to reach criterion performance.

A comparison between performance on the first criterion day of the original eye and the first day of performance for the naive eye shows that although there is a slight decrement in overall performance from 96.6% to 93.3%, this decrement is not significant (correlated $t = 0.55$, d.f. = 2, $P > 0.05$, two-tailed). Further-

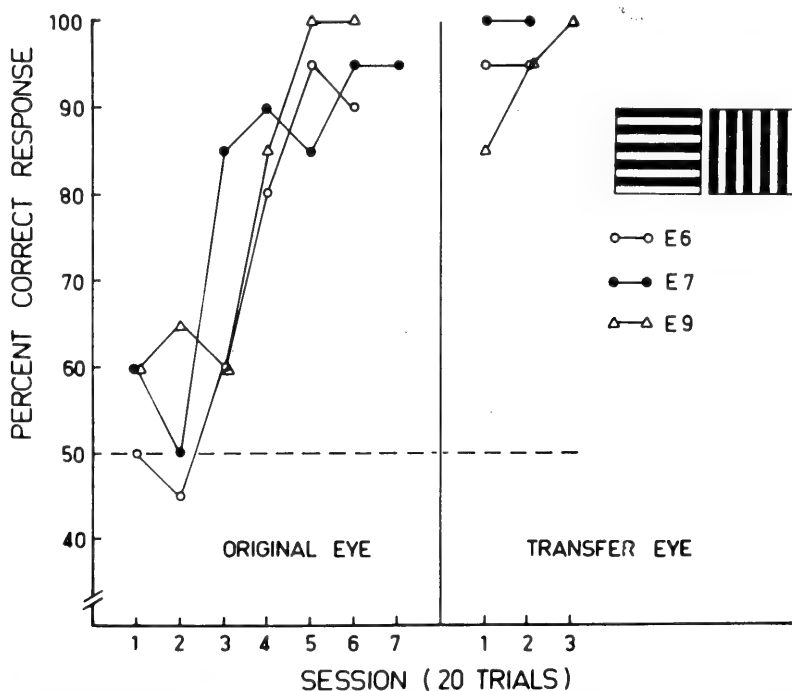


FIG. 5—The left panel shows the performance of three echidnas, with one eye occluded, during acquisition of a vertical-horizontal discrimination. The right panel shows the performance of the same animals with the trained eye occluded and the naive, transfer eye uncovered for the same discrimination task.

more, a comparison between performance on day one of training for the original eye and day one for the transfer eye, shows a jump in performance from 53.3% to 93.3%, indicating that there is a significant (eye) difference in performance and, therefore, that interocular transfer has occurred (correlated $t = 6.10$, d.f. = 2, $P < 0.05$, two-tailed).

DISCUSSION

The results of the experiment show that there is interocular transfer of a vertical-horizontal discrimination habit in the echidna. From inspection of the individual scores from the criterion days of the originally-trained eye to the first day of training on the naive eye, it is clear that this type of orientation discrimination has no significant effect on interocular transfer. In fact, the smaller difference between performances on the first day of criterion for the first (original) eye and on the first day of performance for the naive eye in the discrimination compared to those found for the black-white task, would imply that the extra day of 90% criterion learning acted to stabilize the discrimination habit, and that this stability was passed on to the naive eye.

One other possibility, of course, is that learning set might have influenced performance; that is, the previous experience on the black-white interocular task might have "prepared" them to learn more quickly in this task (Levinson, 1972). However, the length of time it took the animals to acquire the vertical-horizontal discrimination of this particular experiment would imply that learning set was not an important determinant in transfer eye performance. Moreover, it usually takes many two-choice discrimination problems before "insight" reveals itself, even in primates (Harlow, 1959).

EXPERIMENT 5: INTEROCULAR TRANSFER OF OBLIQUE STRIPES

The three echidnas of the previous experiment showed excellent interocular transfer of a fairly easily-discriminable orientation problem. The question then arose: can echidnas also show interocular transfer of the more difficult orientation problem of oblique stripes which are tilted at 45° and 135° with respect to horizontal, that is, oriented at 90° to one another? Lashley (1938) reports that such a discrimination is more difficult for rats under binocular conditions than is the vertical-horizontal task. Levinson and Sheridan (1969) have shown that callosum-sectioned rats do not show complete transfer to the second eye. Levinson (1972) also showed that acallosal guinea pigs do not show complete transfer on this tilt task.

The following experiment was therefore designed to examine (1) interocular transfer of a similar tilt discrimination problem in the echidna and (2) the ability of echidnas to learn an oblique orientation discrimination.

METHOD

(a) *Experimental Animals*

Five animals were used in this experiment: E10, E11, E13, E14 and E15. These animals were from Zoology at Monash University and also from the Canberra area.

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(b) *Discrimination Apparatus*

As for the previous two experiments.

(c) *Stimulus Panels*

Stimulus panels were 26 cm x 26 cm white translucent plexiglas, to which 25.4 mm black electrical tape had been affixed, such that equal stripe widths of black and white alternated across the panel. One panel had the stripes orientated at 45° and the other at 135° to the same horizontal. The panels were back lit with fluorescent lights, as previously described. There were no room lights.

(d) *Training and Experimental Procedures*

The five new animals were trained and run according to the procedures described for the two previous experiments, except that they required a much longer period of familiarization training and handling before they were put into the experimental task. Familiarization training was essentially the same as that described for previous experiments.

All animals were randomly assigned to either the 45° or 135° oblique line condition, and the eye covered for initial training was also assigned on an arbitrary basis, so that there was an even balance between eyes first trained.

RESULTS

The individual performances of the animals are shown in Figure 6. The five animals learned the discrimination to criterion within nine sessions (180 trials).

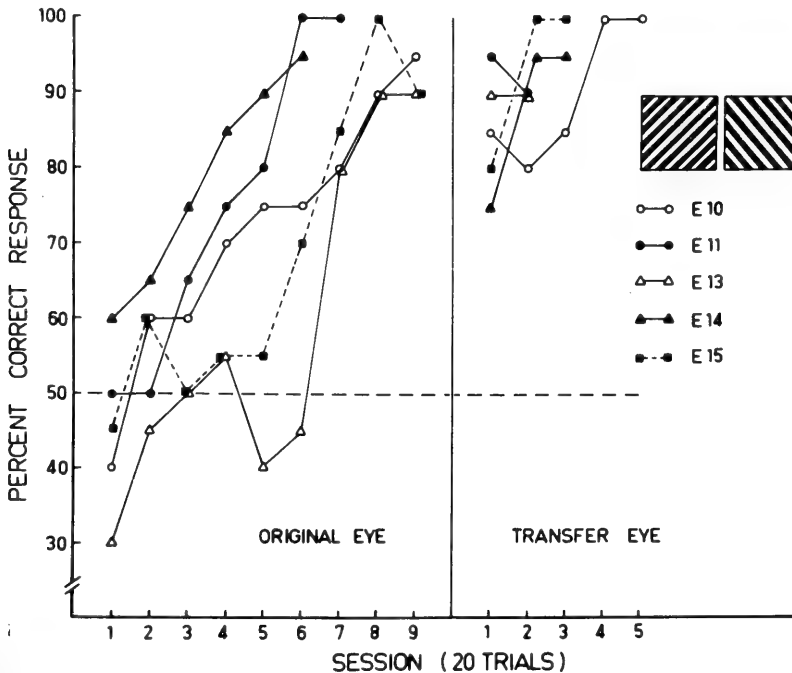


FIG. 6—Individual performances of five, visually-naïve echidnas on an interocular transfer task. The left panel shows % correct performance, with one eye occluded, during acquisition of an oblique stripe visual discrimination. The right panel shows the performance of the same animals with the trained eye occluded and the naïve, transfer eye uncovered for the same discrimination task.

On session one of transfer, all animals showed high levels of correct performance of 75% or better. A comparison between the first day's performance for the original eye and first day's performance for the transfer eye shows that there is a statistically significant difference in performance (correlated $t = 5.39$, d.f. = 4, $P < 0.01$, two-tailed). Moreover, a comparison between the first day of criterion for the original eye and the first day of performance for the transfer eye shows that although there is a fall in mean per cent correct performance from 94 per cent to 85 per cent, this decline is not statistically significant (correlated $t = 2.34$, $P > 0.05$, d.f. = 4, two-tailed). In terms of trials required to reach criterion on the transfer eye, the animals required from two to five sessions (40 to 100 trials) to reach criterion. One animal, not shown here (E12), failed to learn the discrimination after 300 trials.

DISCUSSION

The results of this experiment demonstrate that the echidnas are not only capable of learning to discriminate between lines differing in orientation, but that once this information has been acquired monocularly, interocular transfer of training takes place for the naive eye.

GENERAL DISCUSSION: INTEROCULAR TRANSFER OF INFORMATION

The results of these last three experiments demonstrate that even in the absence of a corpus callosum, the echidna is quite capable of interocular transfer. Several possible anatomical explanations can be put forward to explain such transfer; however, which mechanism or combination of mechanisms is important can only be determined through further experimental work.

Abbie (1939) has shown that the two cerebral hemispheres of the Prototherians (monotremes) are joined by commissural fibres passing by way of the anterior commissure. The electrophysiological study of Allison and Goff (1972) confirms that there is a short latency pathway between cerebral hemispheres in echidna. Although no visual areas have been shown to be interconnected via the anterior commissure in echidna, evidence from the acallosal marsupials (Ebner, 1967, and 1969; Heath and Jones, 1971) in which the anterior commissure is present, suggests that at least part of the anterior commissure may serve as a connecting link between areas subserving visual function. In view of the remarkable similarities of interconnection and structure in the mammalian brain (Mehler, 1969), there is no reason to suspect that the anterior commissure might not also serve a similar function in echidna.

One other possible explanation of interocular transfer involves the uncrossed optic nerve fibres. Lashley (1939) has shown that only a small portion of the total number of neurons in the lateral geniculate nucleus are required to mediate the discrimination of visual patterns, a figure estimated to be 1/50 of the number normally present in each nucleus. The echidna might well be able to support such discriminations as were used in the interocular transfer experiments with the

one percent of optic fibres (Campbell and Hayhow, 1971) which run to the ipsilateral hemisphere.

If the estimate of number of optic nerve fibres (15,000) in the echidna eye is correct (Gates, 1974), then there are at least 150 fibres running to the ipsilateral side of the brain. Although it is not known from which part of the retina these fibres project, these fibres may come from the most central part of the retina (Lashley, 1939). In addition, the same retinal area might be represented in the contralateral visual cortex, thus giving the animal some sort of binocular representation if the contralateral eye also contributes fibres from the same region. Although there is no direct evidence for this notion, the small lateral divergence between the optic axes of the two eyes (Johnson, 1901) would suggest that there is an overlap in the visual fields of the two eyes and, therefore, that there may be binocular interaction.

Muntz and Sutherland (1963) have also shown that rats, which have only a very small number of uncrossed fibres (Polyak, 1957); Lund, 1965), can learn a simple visual discrimination using uncrossed fibres only. Although their data suggest that performance on a more difficult discrimination is not as good when only the uncrossed fibres are used, the results show clearly that once a discrimination habit has been learned, whether it be learned with crossed or only uncrossed fibres, transfer occurs when only the opposite fibres to those employed in training are available. The small number of fibres available ipsilaterally to echidna may be sufficient to do the job as it appears to be in rat. There is a limit, however, to the number of fibres necessary to mediate such a discrimination. For example, Sheridan and Shrout (1966), have shown in albino and hooded rats surgically limited to uncrossed optic fibre pathways, the albinos perform poorly on discrimination tasks in comparison with hooded rats for the same task. Albinos have far fewer uncrossed pathways compared to hooded rats; however, there is no indication of what the actual number (or percentage) of fibres is; therefore, it is impossible to rule out the ipsilateral fibre explanation for interocular transfer in the echidna.

Several other possible "commissural" explanations for interocular transfer may exist. The function of the massa intermedia which joints the two thalami remains unexplained. In addition, the corpora quadrigemina are joined together by a commissure which could pass visual information between the superior colliculi on either side of the brain. Although the colliculus does not appear to mediate pattern vision to any great extent in other mammals (see for example Schneider, 1969), it does subserve visual function and might well be important for transfer of certain types of visual information, for example, brightness discriminations.

RETINOSCOPIC AND OPHTHALMOSCOPIC EXAMINATION OF THE EYE

There is a paucity of description covering the dioptric characteristics and ophthalmoscopic appearance of the eye of the echidna. Johnson (1901, p.36),

reports that although he was successful in obtaining several echidnas to examine ophthalmoscopically, it was only after many "fruitless attempts" that he was able to successfully examine the fundus of the eye of echidna. The difficulty he had in obtaining a view of the fundus is reflected in the rather short account he gives in his monograph.

Routine fundal and retinoscopic examinations were made of the eyes of two echidnas in an attempt to bridge this gap in knowledge.

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

Two echidnas were used for this experiment: one adult echidna weighing 3.45 kg and a younger animal weighing 2.25 kg. Both had been handled prior to this experiment and were therefore reasonably easy to manage.

PREPARATION OF ANIMALS PRIOR TO RETINOSCOPIC EXAMINATION

Animals were deprived of food for 12 hours. Mydriasis was achieved by placing one drop of two% Homatropine Hydrobromide, and one drop of Neo-synephrine (Phenylephrine 10%), in each eye of each echidna one hour prior to examination. This allowed ample time for complete pupillary dilation to be achieved (Davanger, 1971; Smith, 1971).

EXAMINATION

Each echidna was held firmly by an assistant, and an attempt was made to obtain the retinoscopic reflex in the awake animals. However, examination proved to be an impossibility. The animals objected to being restrained and were photophobic. As soon as light reached the eye, the animal would either move its head or close its eye. No attempt to restrain the animal further, or force open its eyelids with fingers, met with success. The animal would struggle even more vigorously or squeeze its eyelids shut. After many abortive attempts each animal was released and allowed to move around in a confined space. Attempts to achieve retinoscopic examination under this non-restrained condition also proved fruitless.

ANAESTHETIC PROCEDURES

The only way to keep an echidna sufficiently quiet for a suitable period of time to carry out retinoscopic and fundal examination was with the help of anaesthetic. Both animals, in turn, were anaesthetized with fluothane. Because the eye retracts back into the bony orbit and rolls medially while retracting in the anaesthetized animal, examination of the eye was made as the animals began to recover from the anaesthetic. This allowed approximately five minutes for examination. Both animals were re-anaesthetized and allowed to fully recover several times in order to recheck findings and to make as broad an examination as possible. Routine fundal inspection was made during two of these recovery periods.

RESULTS AND DISCUSSION

Even after mydriasis had been achieved, the pupillary opening was still small and therefore retinoscopic and fundal examination were difficult to achieve. As the animal began to awaken from the anaesthetic, the eye was pushed forward and rolled laterally by the echidna such that retinoscopic examination could be made. Furthermore, as the animal recovered and began to move its head, the eye protruded even more noticeably. This protrusion can only be likened to the appearance of the eyes in humans who are suffering from thyrotoxic exophthalmos. In this condition, the eyes bulge out in an almost grotesque manner (Vaughan *et al.*, 1968). Retinoscopic examinations made in early recovery and late recovery in the two echidnas are shown in Table 1.

TABLE 1
REFRACTIVE CHANGES IN THE ECHIDNA EYE

Early Recovery	Late Recovery
E(3.45 kg) left eye 0 D*	+3.5D
right eye +0.5D	+4.0D
E(2.25 kg) left eye —.5D	+3.5D
right eye 0 D	+3.5D

* dioptre

A comparison between the refractive state of the eye in early and late recovery shows that a considerable change is occurring in the refractive error of the eye. The eye changes 3.5 to 4 dioptres in this short period of time. This change is interesting as the animal is said to lack the intraocular muscles necessary for accommodation (Walls, 1942; Griffiths, 1968).

THE MECHANISMS OF DIOPTRIC CHANGE

Two explanations exist for this dioptric change. First of all, it is possible that Gresser and Noback (1935) were correct in their subsequently disputed observation that the ciliary body of the eye of the echidna contains muscles which can be used to change the shape of the crystalline lens and, therefore, the dioptric characteristic of the eye (see Gates, 1974). Further histological examination of the ciliary body and related processes is required to confirm or deny the presence of interocular muscles in echidna. If muscles are present, then the change that is seen might be attributed to the effects of the anaesthetic on the muscles attached to the lens, as fluothane is a muscles relaxant (Greene, 1968). When the animal is anaesthetised, the intraocular muscles are relaxed, but when the animal begins to recover from the anaesthetic, the intraocular muscles begin to return to a normal resting state of tonus. The changes seen may reflect the changes in the shape of the lens and, therefore, refractive characteristics of the lens. The bulging of the eye might be viewed as epiphenomenal to the accommodative state.

One thing militating against the above argument is the effect of the mydriatic drugs on the intraocular muscles. The mydriatics used in this experiment are also cycloplegics; that is, they also act on the intraocular muscles to paralyse them. They act such that the anaesthetic does not effect the muscles; therefore, the dioptric changes that occur must reflect some other type of process not involving intraocular muscles. Fortunately, there is at least one other explanation for the refractive changes seen in echidnas.

This second hypothesis argues that the bulging of the eyes is not epiphenomenal to the accommodative change. Although it is difficult to know what function the extraocular muscles are performing during the recovery period, it would appear as though they are forcing the eye, in combination with eyelids, to change its

shape, so that it becomes elongated and, therefore, hypermetropic. This method of eyeball elongation is somewhat reminiscent of the old method used to alter the focus of a camera in which the photographic plate and not the lens is moved (Duke-Elder and Abrams, 1970). It might also be that the change in shape of the eyeball exerts a differential force on the ciliary body, which in turn changes the shape of the lens. It is interesting to note that the nucleus of the oculomotor nerve is very extensive in echidna (Griffiths, 1968). On a basis of size alone, therefore, one might expect extraocular muscles to be well-controlled in echidna. The cartilaginous cup of the scleral layer and the bony plate in the lower lid could well be used as leverage or pressure points to achieve shape changes. Since focal length may be changed externally by a change in the shape of the eye, there may be no need for interocular muscles for accommodation.

Examination of the position of the eye relative to the eyelids in a normally-behaving animal reveals that the eye positions seen under the influence of anaesthesia are similar to those seen in the awake, normal, animal in the natural state. While eating or approaching close-up objects, the eye protrudes forward in a manner similar to that found in the 'late recovery' animal. Under normal conditions, however, the eye does not appear to protrude.

While the measurements of the dioptric state of the echidna eye suggest that the echidna is either long-sighted or normally-sighted in the two eye positions described here, these measurements may not reflect the true or functional dioptric state of the eye. When corrections are made for the error inherent in conventional retinoscopy (Glickstein and Millodot, 1970; see also Gates, 1974 for details of correction) the hypermetropic "bulging" eye appears to be emmetropic or free from refractive error, and the emmetropic, normal eye is myopic or short-sighted. These estimates of the true refractive state of the echidna eye suggest that the eye in its normal, non-protruded state is not used for focus on distant objects, but rather is set up as a diffuse screen for detecting movement. One only has to move an object at a distance from an echidna to get a normal defensive response. Focus under this condition would not be necessary . . . all the animal has to do is detect some change and that change does not have to be defined in terms of a clearly focused image.

FUNDAL EXAMINATION

Inspection of the fundus of the eye of the echidna revealed nothing essentially different from the findings made by Johnson in 1901. The fundus appeared to be a uniform lavender in colour and no blood vessels were visible. The optic disc was plainly visible and was a greyish-white colour. Its shape was oval, the longer axis of the oval lying in the vertical plane. No foveal area was apparent. According to Johnson (1901), the monochromatic appearance of the fundus of the eye of the echidna is reminiscent of that found in fish, amphibia and the hairy armadillo. He also reports that in overall appearance it is reminiscent of the fundus of the eye of dayfeeding birds, without the usual avian cupping and pecten.

CONCLUDING REMARKS

The experiments described here do not purport to demonstrate the function of vision in the echidna in the field, but show instead that this animal has a visual system which is capable of a variety of visual discriminations. In comparison with other 'nonvisual' animals, it would appear as though *Tachyglossus aculeatus* is capable of visual discriminations to a level at least comparable to that of the rat. Moreover, the echidna would appear to have a mechanism for changing the dioptric characteristics of the eye which suggests that its visual system is more sophisticated than the anatomy of its eye would indicate. Although the numbers of myelinated optic nerve fibres in the optic nerve of the echidna are not large (Gates, 1974) compared to those of 'highly-visual' animals such as the primates they are nevertheless substantial. In relation to other 'non-visual' animals, such as bats, which have only a small number of optic nerve fibres, but which behaviourally appear to have reasonable visual functions, echidnas compare favourably.

The experiments on interocular transfer also demonstrate that vision in the echidna has developed to a reasonable degree of complexity, as the left and right hemispheres do not maintain separate 'bits' of information about the visual world, but share such information. The echidna, it would seem is not the ideal natural split brain preparation that superficial examination of its neural structures would suggest.

The important point about the present study is that although it is limited, it clearly shows that echidnas have visual capacity somewhat better than dismal!

Vision has generally been thought to be of little importance to the echidna (Elliot Smith, 1902; Walls, 1942; Griffiths, 1968). Although it apparently relies heavily on olfactory, auditory and tactile sensory information, one might expect that vision is a valuable supplement in the performance of certain activities such as has been suggested for the bat (Suthers *et al.*, 1969). In echidnas, vision might be used for predator detection, location of a food source at a distance, or general orientation, especially because the other sensory systems have either a limited range of effectiveness or are rendered useless for performing such tasks when submerged in the demands of sensory input of another task. For example, the echidna might use its eyes for 'watching' the surrounding environment while its olfactory, tactile and auditory systems are involved in the task of feeding. Flat corneas and protruding eyes probably give the echidna a panoramic view of the world unobstructed by anatomical features immediately peripheral to the eye. Such a system could be an efficient predator detection device. Although capacity does not imply use, the findings of the present report suggest that such function might be worthwhile exploring in echidnas.

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Volumetric Analyses of Monotreme Brains

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INTRODUCTION

The volumes of eleven brain structures — (medulla oblongata, cerebellum, mesencephalon, diencephalon, and the following divisions of the telencephalon; neocortex, schizocortex, hippocampus, septum, paleocortex-amygdala complex, bulbus olfactorius and the striatum) of the platypus and of the echidna were calculated. The volumes of the same eleven structures have been calculated previously for insectivores, bats and primates (Stephan and Andy 1970, Stephan and Pirlot 1970, and Pirlot and Pottier 1977). Complete details of the methods used can be found in these publications. In this paper we comment briefly on the shape of some of these structures in the monotremes and especially on some of the histological characteristics of the cortex.

The organization of the cortex in Monotremes has been described in detail by Abbie (1940). We will not comment here on his morphological subdivisions, although we found it somewhat difficult at times to recognise in our specimens all the variations that he has distinguished. Only two cortical layers are of special interest: layer II, which is well marked, as is usual in mammals, and layer V (which may appear to be layer IV in several places, due to the indistinctiveness of III and IV).

MATERIAL AND METHODS

One specimen of *Ornithorhynchus anatinus* (body weight 1040 g, brain weight 9.169 g) and one of *Tachyglossus aculeatus* (body weight 4720 g, brain weight 27.518 g) were perfused with saline and then 20% formalin. They were stored for a week in 10% formalin, then dissected out, weighed, embedded in paraffin wax, and cut serially at 10 μ . Every fifth section was stained with Nissl. For each species, 100-200 of these sections were photographed and the measurements of area and the volumes were made from these photographs (See Stephan and Pirlot, 1970 for details). These photographs were also used in the estimates of the length of some brain structures.

For comparison, the brain of one *Didelphis marsupialis* (body weight 1205 g, brain weight 6.885 g) was treated in the same way.

The measurements of cells were made using a Zeiss-Jena NU 2 microscope with a micrometer in a 12.5 x eyepiece and with a 50 x objective.

HISTOLOGICAL FEATURES OF THE CORTEX

The platypus brain is lissencephalic, the rhinal fissure being the only land mark on its surface. In contrast, the echidna brain is gyrencephalic with well-marked fissures. Neither brain, unlike those of many lower mammals, shows a clear separation into neocortex (isocortex), paleocortex (allocortex), or mesocortex (juxtallocortex). This is of some interest as the *Didelphis* brain does show such subdivisions, particularly a well differentiated intermediate area (mesocortex) described by Oswaldo-Cruz and Rocha-Miranda (1968) as a piriform cortex. Thus, there is less histological differentiation of the monotreme cortex than there is in *Didelphis*.

Platypus

Under the outer plexiform layer I, there is a well marked layer II, which is 60-70 μ thick and in which the rounded medium sized cells (larger than granule cells) are densely packed. The dense layer V has an irregular width, and contains rounded or ovoid cells and a considerable number of larger, usually ovoid neurons. Some of the larger cells have subpyramidal shapes. The number of these cells in a one centimetre square of the micrometer at 312.5 x magnification is around 20 in the platypus (cf. 45 in the echidna).

An interesting feature of the cortex, is the existence of a well developed schizocortex-like area in the vicinity of the hippocampus, i.e. in the subicular-

TABLE 1

A. CELL SIZES IN PLATYPUS (SECTION 662)			
	Mean diameters	Diameter ranges	Mean smaller/greater
Layer II	11.90 x 10.43	16.24 - 6.09	87.6%
Layer V	12.11 x 9.38	22.33 - 6.09	77.4%
B. CELL SIZES IN ECHIDNA (SECTION 1656)			
	Mean diameters	Diameter ranges	Mean smaller/greater
Layer II	12.26 x 8.36	20.30 - 6.09	68.2%
Layer V	14.75 x 10.89	24.36 - 6.09	73.8%
C. CELL SIZES IN DIDELPHIS (SECTION TO PLATE 6 IN OSWALDO-CRUZ AND ROCHA-MIRANDA, 1968)			
	Mean diameters	Diameter ranges	Mean smaller/greater
Layer II	16.95 x 10.52	24.36 - 6.09	62.0%
Layer V*	16.70 x 11.11	28.42 - 6.09	66.5%

* Or equivalent in position. In all cases, N = 100. Measurements in μ m. Magnification for measuring: 50 x 12.5 = 625 x. The repetition of some figures (e.g. 6.09) indicates the limit of precision that could be attained in reading the micrometer scale (1 division = 2.03 μ m).

retrosplenial area. In contrast to the data in bats, there is no schizocortex in the lateral region of brain between paleo- and neocortex.

Echidna

Under the outer plexiform layer I, layer II is 70-90 μ thick and contains medium sized cells which are mostly ovoid though sometimes rounded. This layer is usually much less dense and less well marked than the corresponding layer in the platypus, but in some rhinencephalic regions, it is denser and can be separated into a layer IIa, which is narrower and less dense, and a layer IIb, which is broader and denser. Layer V varies considerably in thickness. It contains medium sized cells intermingled with granule cells and with a number of larger neurons, some of which are pyramidal. The number of the large cells in a one centimetre square of the micrometer at 312.5 x magnification is about 45 (cf. 20 in platypus).

In the echidna, as in the platypus, a schizocortex-like area is found in the subicular-retrosplenial area, near both dorsal and ventral extremities of the hippocampal arch, but no lateral schizocortex is present.

CELL MEASUREMENTS

The mean lengths were measured of the two diameters of a random sample of 100 cells from layer II and from layer V at the level of the anterior commissure and the upper lateral (orbital) region of neocortex. The measurements from the three species are shown in Table 1. Here it can be seen that the cells in layer II are more rounded in the platypus than in the echidna. The smaller diameter of the cells is 87.6% of the length of the cell's larger diameter in the platypus while in the echidna, the same proportion is 68.2%. In layer V, the proportion for the platypus is 77.4% and that of the echidna 73.8%. A possible interpretation of measurements, is that in layer II the more rounded cells of the platypus are of a younger shape than those of the echidna, whereas in layer V all cells are of the mature type. This interpretation is supported by the differences in the density of layer II between the platypus and the echidna. The dense cellular arrangement of layer II in the platypus is probably much closer to the embryonic condition than is the more open arrangement of cells in the echidna. In this sense, the platypus cortex could be termed more primitive than that of the echidna.

Didelphis

It is interesting to compare the monotremes with the reputedly primitive, subplacental mammal, *Didelphis*. A detailed description of the brain of *Didelphis* is outside the scope of this paper, but the following points are of interest.

Under the outer plexiform layer, there is a fairly consistent pattern at most levels from rostral to caudal cortex. Using the section upon which plate 6 in Oswaldo-Cruz and Rocha-Miranda (1968) is based, it can be seen, that in the orbital (dorso-lateral) region, layer II is 80-120 μ thick, is moderately dense and contains large ovoid (sometimes rounded) cells. In the piriform (ventro-lateral)

region, this layer is much denser, and two layers can be distinguished — an external layer with rounded cells and an internal one with elongate or spindle-shaped, radially oriented cells.

Underneath layer II, the organisation varies according to the level and to the region. In a general way, especially in the orbital region that most resembles what we have observed in the monotremes, the area corresponding in location to layer V of the platypus and the echidna, shows a moderately dense assemblage of cells of various diameters, generally having a globulous or ellipsoid shape.

The differing diameters of cells shown in Table 1 were tested statistically to see if the differences between layers and between species were significant (Table 2).

TABLE 2
DIFFERENCES BETWEEN GREATER DIAMETERS

Between mean differences tested	Significant (s) or non-significant (ns) by Mann-Whitney test at 5% level
A II - B II	NS
A II - C II	S
B II - C II	S
A V - B V	S
A V - C V	S
B V - C V	S

SHAPE OF BRAIN AND BRAIN STRUCTURES

A rather vague statement was made by Ziehen (1897, p.34) who writes 'Das Kleinhirn (in *Ornithorhynchus*) wird von den Grosshirnhemisphären noch weniger als bei *Echidna* überlagert'. This suggests that in polar view the hemisphere occupies more of the total brain-length in the echidna than it does in the platypus. However, from our serial sections, we calculate that hemispheres of the platypus occupy 82.0% and that of the echidna 81.5% of the length of the cortex plus cerebellum. (There was little difference in the volume shrinkage of the brains as a result of the embedding process — 63.5% for the platypus and 61.5% for the echidna). Thus, the percentage of the brain length occupied by hemispheres and by cerebellum (17%) is the same for both species. What was not described accurately by Ziehen (1897) is that the cerebellum reaches further forward *under* the hemispheres in the platypus than it does in the echidna, so that the real percentage of total length occupied by the cerebellum should be 34% in the platypus and 23% in the echidna. This corresponds well with our volume estimates (Table 3).

There are two other structures in the platypus which also show a long rostro-caudal extension. The striatum extends over 60.2% of the hemisphere length in the platypus and 33.3% in the echidna. This does not agree with the volumetric

MONOTREME BRAIN VOLUME

TABLE 3

ABSOLUTE VOLUMES OF VARIOUS BRAIN STRUCTURES AND THEIR PERCENTAGE OF TOTAL BRAIN VOLUME

	PLATYPUS		ECHIDNA		OPOSSUM	
	Abs. vol. mm ²	% of total brain	Abs. vol. mm ²	% of total brain	Abs. vol. mm ²	% of total brain
Neo	4099.28	47.83	11,372.4	42.79	1442.88	22.24
Scz	121.34	1.41	396.9	1.49	—	—
Hip	506.16	5.90	1773.5	6.65	527.88	8.14
Sep	52.33	0.61	108.6	0.41	59.82	0.92
Pal	505.56	5.89	5374.5	20.33	779.75	12.02
Bul	71.37	0.83	835.8	3.14	572.13	8.82
Str	478.21	5.58	1553.5	6.68	240.30	3.70
Di	1050.97	12.27	1768.3	5.84	607.82	9.37
Mes	163.56	1.91	686.7	2.58	373.03	5.75
Cbl	919.55	10.74	1589.3	5.98	839.07	12.93
Med	163.56	1.91	686.7	2.58	572.13	8.82
Mes	—	—	—	—	473.08	7.29
	8571.45	100.00	26,578.2	100.00	6487.89	100.00

The structures in order from top of column are: neocortex, schizocortex, hippocampus, septum, paleocortex, bulbus olfactorius, striatum, diencephalon, mesencephalon, cerebellum, medulla oblongata and mesocortex.

measurements in Table 3. The hippocampus has a rostrocaudal extension of 54.2% of the hemisphere in the platypus and 42.6% in the echidna. This again differs from the volumetric measurements. The misfits between lengths and volumes are of course due to differences in the shape of the structures.

VOLUMETRIC MEASUREMENTS

Table 3 sets out the absolute volumes of each of the eleven brain structures measured and the percentage that that volume represents of the total brain volume. In previous studies on placental animals a placental with little neocortex was used as a "basal" animal with which to compare the degree of development of brain structures in the "higher" placentals, (see Stephan and Pirlot 1970 for bats, Stephan and Andy 1964 for primates). We have no 'basal' monotreme. However, for interest, Table 4 shows the relative percentage of the various brain structures for 'basal' insectivores, the platypus, the echidna, the American opossum and the prosimians (basal insectivore and prosimian data from Stephan and Andy 1964).

1. The neocortex of the platypus is slightly larger relatively than the echidna, and this is surprising as the platypus brain is lissencephalic while that of the echidna is gyrencephalic.

2. The striatum and the hippocampus are of equal size relatively though slightly larger in the echidna in spite of the greater rostro-caudal extension of both components in the platypus.
3. The bulbus olfactorius is relatively underdeveloped in the platypus compared to the echidna, which might be expected for an aquatic animal.
4. Similarly the paleocortex (+ amygdala) is smaller, relatively, in the platypus than in the echidna.
5. The diencephalon is much larger in the platypus, probably as a result of its greater sagittal extension in the platypus.
6. The mesencephalon is relatively small in both animals when compared with many other mammals.
7. The larger relative size of the cerebellum in the platypus is no doubt related to its three dimensional movements in water.

TABLE 4

VOLUMES OF SUBDIVISIONS OF THE BRAIN IN % TOTAL BRAIN

	BASAL INSECT	PLATYPUS	ECHIDNA	PROSIMIAN
NEO	13	48	43	54
SCZ	3	1	1	2
HIP	9	6	7	4
SEP	2	1	1	1
PAL	19	6	20	4
BUL	10	1	4	2
STR	5	5	6	5
DI	8	12	6	8
MES	6	2	2	3
CBL	12	11	6	12
MED	13	7	4	5

Abbreviations as in Table 3.

DISCUSSION

1. DIFFERENTIATION OF THE NEOCORTEX

The various layers in the neocortex of the platypus and the echidna are roughly similar although some differences in thickness and density do exist. The most important difference is probably the greater abundance of large (sometimes pyramidal) neurons in the medial half of layer V in the echidna. We are inclined to believe that this suggests an advance in cortical organisation. This need not necessarily also suggest that the echidna is a more progressive mammal than the platypus.

2. PRESENCE OF A SCHIZOCORTEX

The restriction, in both monotremes, of the schizocortex to the subicular-retrosplenial areas is remarkable. By the way of contrast, the bats have a schizocortex that may extend behind and around the hippocampal formation to the lateral edge of the brain, between paleo- and neo-cortex. It is generally agreed that all schizocortex is of archipallial origin. The medial (subicular) portion represents an earlier development than the lateral one, probably both in ontogeny and in phylogeny. This is not surprising considering the original dorso-central and paramedial position of the archipallium. The extension of that component, or of its derivative (schizocortex) towards the lateral regions, probably is the final stage of its quantitative and topographic evolution before it became reduced in size in higher mammals — (see Stephan and Andy 1970).

3. IDENTIFICATION OF AN INTERMEDIATE CORTEX

The most striking cortical difference between our monotreme brains and that of *Didelphis* consists in the latter possessing a very distinct *piriform cortex* between paleo- and neo-cortex (see Oswaldo-Cruz and Rocha-Miranda 1968). As mentioned previously, the piriform region is characterised by a double layer II of very densely packed cells. Such a high accumulation of cells, most of them oriented in the same direction, reminds one of an immature, even embryonic, tissue. Pirlot (1975), in a study of the South American Edentate *Dasypus* tentatively termed such an organisation "mesocortex". We did not find a distinct piriform mesocortex in the monotremes studied, but the organisation of layer II in both monotremes reminds one of an "unachieved cortex" — a condition close to that of a "mesocortex". There is a common relatively primitive appearance of piriform, mesocortical and monotreme cortices. Thus, although the cortices of lower placentals, marsupials and monotremes each show unique characteristics, they share the same general form. In general, the platypus and the echidna have a relatively undifferentiated cortex and may be considered "paramesocortical" animals.

4. OLFACTION

A special remark must be made concerning the olfactory structures of the brains studied in this paper. Considering firstly the bulbs, from *Platypus* (0.83%) to *Tachyglossus* (3.14%) and *Didelphis* (8.82%), we have an ascending order of size that probably corresponds to an increasing order of use of that organ. A similar hierarchy (with more modest figures ranging from 1.61 to 3.92%) was found previously among 43 species of bats showing various degrees of usage of olfaction (Pirlot and Pottier, 1977). In Edentates too, the same observation was made in the case of a species using (6.7%) and one not using (2.3%) olfaction for food detection (Pirlot 1975). But it is important to note that, in all mammals mentioned above, there is no necessary close correlation between the size of the so-called rhinencephalon (paleocortex + amygdaloid region), the size of the bulbus olfactorius and the observed olfactory ability of the animal. We would say that an animal with good olfactory capability has above all a well developed peri-

pheral organ, i.e. olfactory bulbs. Behavioural reduction of olfaction goes along with reduction in bulb size. It is likely to be correlated also with some limited reduction of the rhinencephalon. However, the latter may be quite large even in the case of moderate use of olfaction. Its oversize in *Tachyglossus* is nevertheless intriguing.

5. PRIMITIVENESS AND PROGRESSIVENESS

It should be emphasised that it is very difficult to isolate criteria that clearly establish the "primitiveness" of monotreme brains. However, it is important to attempt to determine which criteria are plesiomorphic and which are apomorphic. In placentals, progressiveness, is measured by the progression index which is the ratio of brain size in the animal examined compared to the brain size of a 'basal insectivore' of the same body weight. We have no reference type for an allometric comparison of brain components in Monotremes.

The cortex could be considered to be among the most primitive mammalian cortices on the basis of the low number and low density of large, especially pyramidal, neurons. It is thus surprising to find that a very high proportion of cortex is neocortex. This does not necessarily mean an advanced degree of progressiveness, although the two are usually related. Among the chiroptera, Stephan and Pirlot (1970) and Pirlot and Pottier (1977) found the following serial values for the neocortical percentages and progression indices: insect eaters 18.85% and 202; nectar feeders 22.84% and 326; frugivorous microchiroptera, 26.38% and 376; frugivorous megachiroptera 29.34% and 429; piscivorous 31.32% and 549; carnivorous 29.95% and 630; sanguivorous 34.50% and 667. The neocortical percentage for the platypus is 47.83% and for the echidna 42.79%, so that we would expect that the progression indices for these two species, if such indices were available, would be about equal. Jerison (1973) uses another ratio, encephalisation quotient in comparing the relative volumes of mammalian species. His figures are; basal insectivores 0.25-0.40; monotremes 0.50-0.75; prosimians 0.7-2.0; higher primates 1.5-7.8.

In all methods, there is a clear indication that monotremes have relatively high brain and neocortical indices. Size alone cannot be taken as a criterion for progressiveness unless a group of related forms, that is forms having a broadly similar organisational brain structure, are being considered. There are obvious qualitative differences between the brains of monotremes and other mammals and this of course will prevent simple comparisons between the two on the basis of quantitative component analysis. It is only within the general framework of a common structural type that quantitative differences can be related to ecology and behaviour, as was done in the studies on chiroptera. Further as Pirlot (1970) showed in a review of data from Insectores, Primates and Chiroptera, even the brain to body ratio cannot be interpreted in a purely quantitative way without considering the differing life habits of the animals.

Thus the two species both show a high neocortex percentage, with the platypus only slightly higher. Most of the brain structures are equally developed in both

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forms, except that the echidna has greater development of the smell areas (bulbus olfactorius and paleocortex) while the platypus has greater development of the cerebellum. This is what one would expect, smell being important to the terrestrial echidna but relatively unimportant to the water and burrow living platypus, whereas a sense of balance is of greater importance to a platypus swimming in the water than to the echidna walking on land.

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Some Aspects of the Ecology of the Platypus, *Ornithorhynchus anatinus*, in the Upper Shoalhaven River, New South Wales

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ABSTRACT

The platypus in the study area on the upper Shoalhaven River in New South Wales were found to be carnivorous, feeding mainly on insect larvae found in the river benthos. The weights and tail volumes of animals showed a marked decline in the winter months and this may be due to the added thermal stress imposed by the colder water temperatures at these times. Heavier stages of moult of the fur occurred predominantly in the months in which water temperatures were highest.

The main part of the study area was found to have a resident population of at least 14 to 18 individuals, most of which appeared to move only up to around 400 metres from their point of original capture. However, some platypus moved over distances in excess of 1 kilometre in only a few days. Some members of the resident group were caught as many as 10 times after their initial capture, while other animals were captured once, and not again during the study. The latter were considered to be transients.

INTRODUCTION

The platypus, *Ornithorhynchus anatinus*, is a common inhabitant of many of the lakes, rivers and streams of the eastern Australian mainland and Tasmania. In spite of it being a regular part of the ecological composition of the waterways of eastern Australia, the study of the ecology of the species has been almost totally neglected.

Apart from some valuable unpublished data collected by Temple-Smith (1973) during a study of the reproduction and venom apparatus of the platypus, ecological data on the species have been restricted to observations by early naturalists (Bennett, 1860 and Burrell, 1927).

The present study, initiated during an investigation of some aspects of temperature physiology of platypus (Grant and Dawson, 1978 a & b) concerns the ecology of platypus occupying an area of the upper reaches of the Shoalhaven

River in New South Wales. The work is continuing, but enough data has been collected at this point to allow discussion of some aspects of the ecology of the platypus in the study area.

MATERIALS AND METHODS

The study area on the upper reaches of the Shoalhaven River in New South Wales consists of a series of deep pools interconnected by riffle areas of varying lengths. Most of the trapping was carried out in two pools and one series of riffles totalling 1.8 kilometres of river bed. These sites were trapped intermittently during 1973, 1974 and 1975. In 1976 and 1977 these two pools were sampled at least bi-monthly. Two sites were trapped in the larger of the two pools (940 metres long), one being trapped with two 50-metre nets from an hour before darkness until an hour after daylight the following day, and the other being trapped with the same nets from an hour before darkness until 0100 or 0200 hours the following morning. The single site on the smaller pool (500 metres long) was netted with one 50-metre net from dusk until 0100 or 0200 hours.

The whole study area extended along 6.8 kilometres of the river and 3.2 kilometres up the adjoining creek. A number of pools in the area (upstream and downstream from the main area) were trapped once or twice in 1977, and three sites on the creek were netted in February, 1978, from around dusk until 0100 or 0200 hours. Variable numbers of nets were used, depending on the size of the pools. The platypus were captured in unweighted fishing nets and were released with numbered stainless-steel bands attached to their hind legs (Grant and Carrick 1974). In 1975 aluminium bands were used, but this practice was discontinued at the end of that year when marking of platypus with both stainless-steel and aluminium bands demonstrated that the animals were able to remove the latter. In 1977 narrow bands (0.5 cm) were used on all male animals, as the wider bands (0.8 cm) were found to make an indentation in the base of the spur in some individuals. Double banding of some platypus, with both wide and narrow bands on opposite legs, demonstrated that the platypus could not remove the narrow bands over a period of several months. Spur wear was also much reduced by the use of the narrow bands.

During four different experimental periods (two in summer and two in winter) eight to 17 platypus were marked with brightly coloured adhesive tape attached to their tails, and the movements of these animals were followed for eight to 10 days after their release. Two separate observers walked night and morning for distances of 1.3 kilometres upstream and 2.0 kilometres downstream. The time and location of any platypus marked with the coloured tape were recorded.

Every platypus caught throughout the study was weighed when dry. Platypus caught during 1976 and 1977 were lightly anaesthetised with ether and the following data collected:

- A. Cheek pouch contents. These were removed with a small spatula and fixed in 70% ethyl alcohol for later analysis of food selection.
- B. Body weight.
- C. Tail Volume Index, TVI (a graded estimate of tail fat reserves). This was estimated for each individual using criteria based on a range of platypus previously measured. The tail of the platypus is a fat storage area with large fat deposits around the muscles of the vertebral column. These give the tail its shape, and shape gives some indication of the amount of fat stored. The categories, in order from most to least fat, were:
 1. Tail turgid with the ventral side convex.
 2. Tail able to be folded slightly at lateral edges. Ventral side flat. Rest of tail turgid.
 3. Lateral edges of tail easily rolled. Ventral side slightly concave. Rest turgid.
 4. Whole tail able to be folded along ventral midline. Whole tail soft.
 5. Vertebrae showing through tissue on ventral side. Whole tail soft.

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- D. An estimate of moult on dorsal and ventral surfaces of the body was also made for each animal, using the following criteria:

none — guard hairs of pelage intact.
very light — small groups of guard hairs missing. Noticeable only on dry animal.
light — patches of guard hairs missing. Often noticeable only on dry animal.
moderate — large patches of guard hairs missing. Usually noticeable on wet animal.
heavy — pelage almost devoid of guard hairs. Always noticeable in wet animal.

- E. In October, December and February of 1977-78 female platypus were injected with synthetic oxytocin (Syntocinon, 1 international unit per kilogram of body weight) to determine whether or not they were lactating.

Up to February, 1978, only 4 juvenile platypus (1 male and 3 females) were caught in the study area. Body weights, TVI and moult data for adults only have been included here.

Trapping sites on the Shoalhaven River were located on aerial photographs of the area, and distances between the sites were measured from these (scale 1:7,000). Distances along the creek were measured on a 1:25,000 topographical map. Areas of the pools were measured on aerial photographs using a planimeter (Coradi). River heights were obtained from the Water Resources Commission from their gauging station in Warri, downriver from the study area. No major rivers enter the Shoalhaven River between the study area and Warri, so that the heights recorded reflect similar events in the study area.

RESULTS

FOOD

The proportions of the various food species found in cheek pouches sampled at the four seasons of the year are shown in Table 1 and a more detailed analysis of the food material recovered from cheek pouches of platypus captured in the

TABLE 1
SEASONAL VARIATIONS IN FOOD ITEMS IN PLATYPUS CHEEK POUCHES

<i>Food Item</i>	<i>Summer</i> (n=11)	<i>Autumn</i> (n=17)	<i>Winter</i> (n=16)	<i>Spring</i> (n=16)
<i>Insect (larvae)</i>				
Trichoptera	64%	56%	41%	53%
Odonata	9	19	0	12
Diptera	18	25	12	6
Ephemeroptera	0	0	18	24
Megaloptera	9	0	0	0
<i>Non-insect (adult)</i>				
Nematomorpha	0	0	17	0
Decapoda	0	0	12	0
Anura	0	0	0	5

n = number of pairs of cheek pouches examined.

The numbers in columns refer to the percentage of cheek pouches in which the food item listed at left was the dominant constituent.

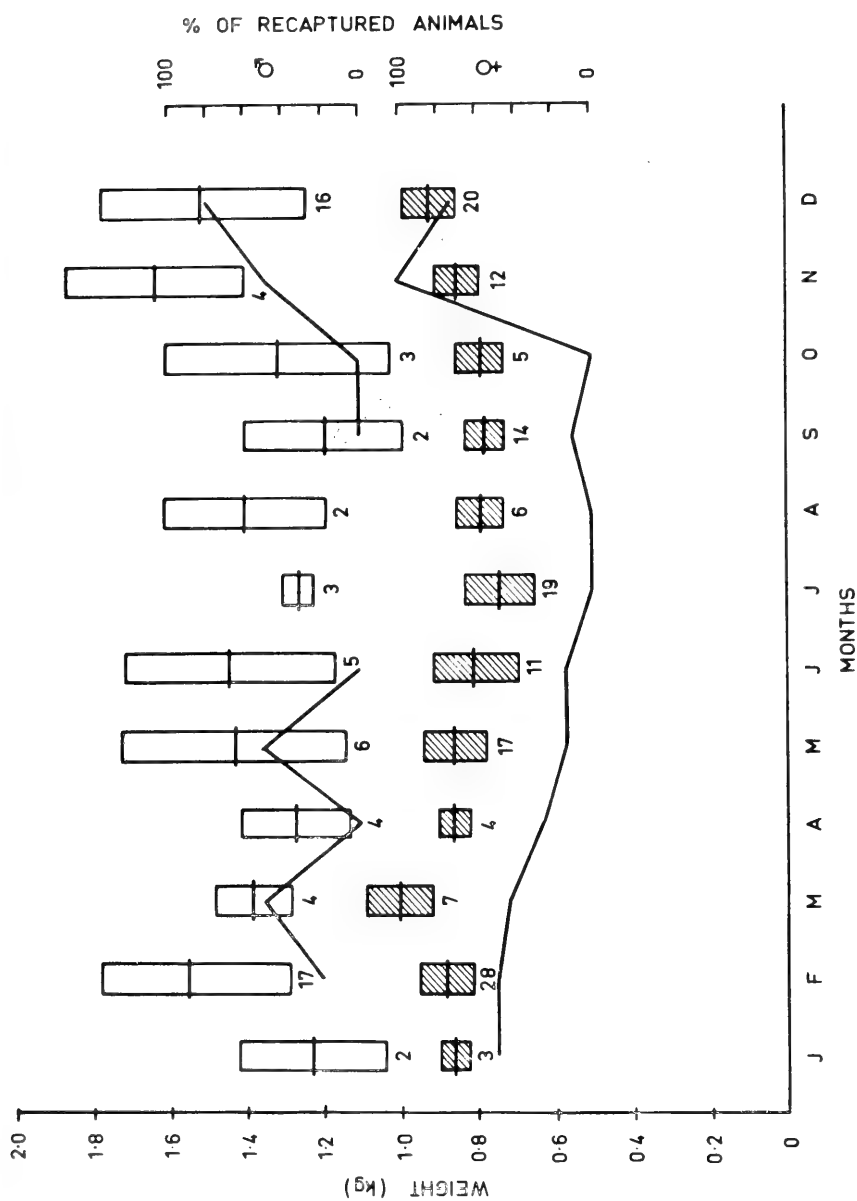


FIG. 1.—Monthly weight changes in platypus. Horizontal lines indicate monthly mean weights for platypus caught in the study area 1973-77. Rectangles enclose two standard deviations; open rectangles indicate males, hatched rectangles indicate females. Lines indicate the percentage of platypus recaptured at various months of the year which were at their maximum weight in those months.

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study area are presented elsewhere (Faragher, et al., 1979). These data indicate that the platypus in the study area were feeding predominantly on benthic larvae of various insects. However, in winter 29% of the cheek pouches sampled contained non-insect invertebrate material as their dominant constituent, and one platypus was found to have some skin and several fragments of long bones from a frog in its cheek pouches.

BODY WEIGHT AND TAIL VOLUME INDEX (TVI)

The body weights of male and female platypus captured in the study area were found to fluctuate from month to month (Fig. 1). The fluctuations seen in mean male weights were not closely related to time of the year, although animals caught in the late spring (November) and summer (December and February) tended to be heavier than those caught at other times of the year. However, no statistically significant difference was found between the mean weights of males on a monthly basis (one-way analysis of variance, $P > 0.05$). The sample sizes for males may have been too small to show any marked trend in weight variation. Mean monthly weights for female platypus showed significant variation ($P < 0.01$). Females were at their peak weight in early autumn (March), after which their mean weights declined gradually to a minimum in mid-winter (July) and began to rise again in November with the onset of warmer conditions.

Twenty-six female platypus and eleven male platypus were recaptured in the whole study area after being marked. These recaptures occurred in most of the months of the year, although no single animal has been caught in every month. Fig. 1 shows the percentage of platypus caught each month which had their maximum recorded weight in that month. Again the data for males is confusing. No males were recaptured in the late winter months, and although 50-80% of male platypus recaptured in November and December were at the maximum recorded weights in those months, animals recaptured in April, May and June showed no clear trend in their weight variation. The data for females showed that the recaptured animals' weights fluctuated in a manner similar to the mean weights of all animals caught. Fifty to 75% of female platypus recaptured in the summer months of December to February achieved their maximum weights in those months, while in the winter and early spring months of June to October less than 15% of the animals recaptured were at the maximum weight recorded for those individuals. The peak in mean weight for females in March was not indicated in the data for recaptured animals. All female platypus recaptured in November exhibited their maximum weights in that month, while the mean weight of all females caught was only beginning to rise to around the summer level in November. Obviously the analysis of the data for recaptured animals is complicated by the possibility that an animal may not be caught in the month in which it would normally be at its actual maximum weight. In spite of this limitation, Fig. 1 does indicate that both the weights of recaptured female platypus

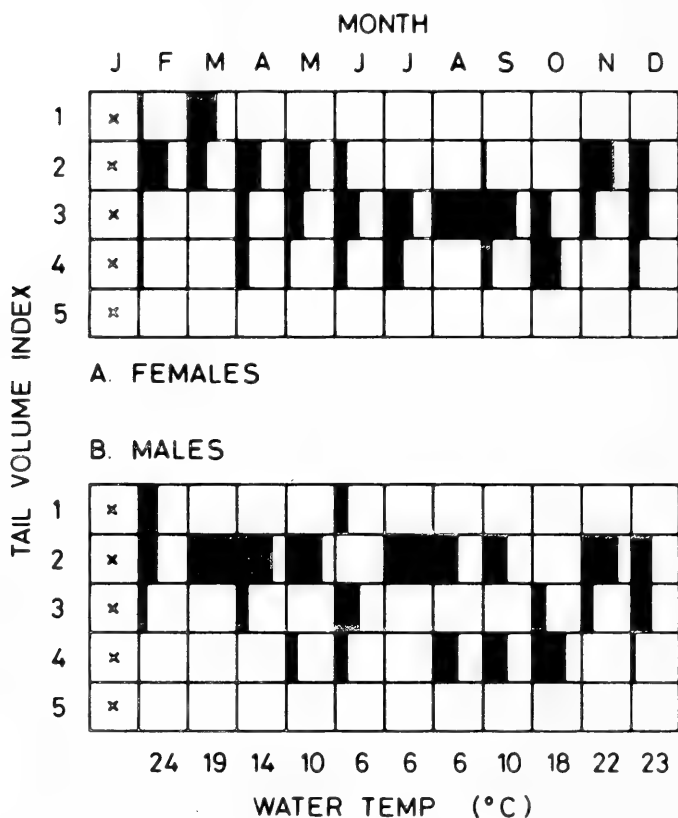


FIG. 2.—Tail Volume Index (TVI) of platypus caught at various months of the year. Width of shaded areas indicate the percentage of animals caught each month which had TVIs in the respective category at left. Mean water temperature recorded during trapping periods is shown under B.

and the mean weights of all females caught at each month showed a similar trend in seasonal body weight changes. One particular female, caught 10 times at regular intervals during the various years of the study, clearly illustrates this annual weight cycle: Jan. 1975 (wt = 870 g.); Feb. 1975 (825); Apr. 1977 (880); June 1975 (750); July 1973 (700), 1976 (700); Aug. 1976 (750); Sept. 1976 (815); Dec. 1976 (890), 1977 (900). This animal showed a definite decline in weight from late spring into the winter months, followed by an increase from early spring into summer.

Platypus in the study area showed less variation in their tail fatness than animals caught in other areas (unpublished data), where both extremes of Tail Volume Index (TVI) have been found. No platypus caught in the study area

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had tails in condition 5 (i.e. with the tail completely flaccid and with vertebrae showing through the tissues on the ventral side). Similarly, tails of category 1 were not common.

Fig. 2 shows annual variations in platypus TVI. Female platypus were found with TVI 1 only in the months of February and March, when mean weights were also high (Fig. 1). A spread of TVIs was found in animals caught in any month, but the highest percentages of animals with tails of categories 1 and 2 were found in summer, autumn and early spring. More animals with tails of categories 3 and 4 were found in the winter months. This was a clearer trend in females (Fig. 2 A). Males seemed to retain more of their tail fat reserves during the colder months. Although 40% of the male platypus caught in February had TVIs of 1, and the highest mean weight of males was recorded in that month, 30% of males caught in the winter month of June also had tail fat reserves in excellent condition (Fig. 2 B).

MOULT

Very little moulting was found on the tails of platypus in the study area, and the insulation properties of the tail fur are quite poor, especially when the animal is in water (Grant and Dawson, 1978 b). For these reasons only dorsal and ventral body moult patterns were considered.

Fig. 3 shows the annual patterns of moulting in both male and female platypus. Very few animals captured were more than moderately moulted in the winter months, and most females caught in these months showed only light moult. The ventral pelage in both sexes was usually found to show less than light moulting, and heavy moult was only seen in animals in spring or early summer, when water temperatures were beginning to rise (water temp. is shown in Fig. 3 B). The lack of extensive moult on ventral surfaces at any time of the year is not surprising as the ventral pelage contributes more to the body insulation than does the dorsal fur (Grant and Dawson, 1978 b). Moderate moulting of the ventral pelage was seen only in the spring.

MOVEMENTS

Platypus marked with coloured tape and followed over periods of 8 to 10 days after their release were found to move some distance within the pools in which they were caught. Four animals were observed to move freely between the two pools of the main part of the study area, but only one platypus was sighted outside these two pools during four observation periods covering 3.3 kilometres of river. In this instance the animal had moved from trap site 6, upstream to the pool of trap site 4 (a distance of 1.3 kilometres, see Fig. 5) in six days. Fig. 4 shows the number of marked animals which moved various distances from their point of release. Most of the animals resighted (60-80% of those released) moved less than 400 metres during the observation periods.

Trapping studies, carried out in 1977 outside the main part of the study area, showed a similar limited movement by many platypus in the area. Very

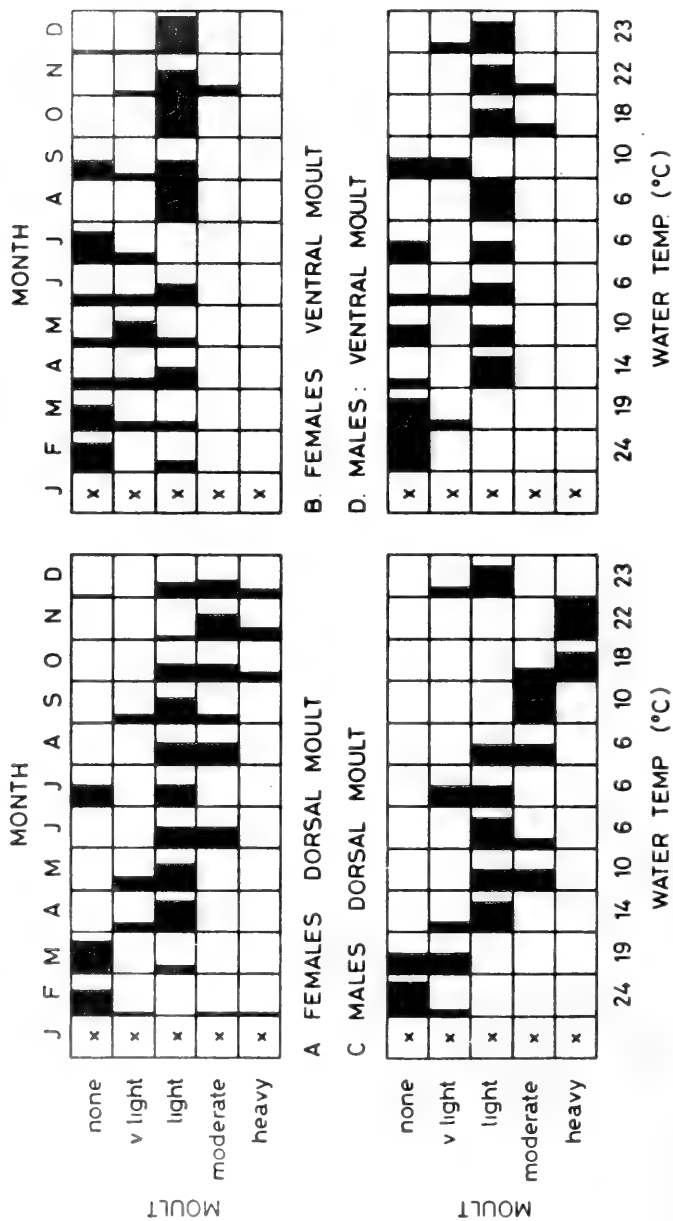


FIG. 3.—Annual moulting patterns in platypus. Each shaded area indicates the percentage of animals caught each month which showed the stage of moult indicated at left. Mean water temperatures are shown below each month's column.

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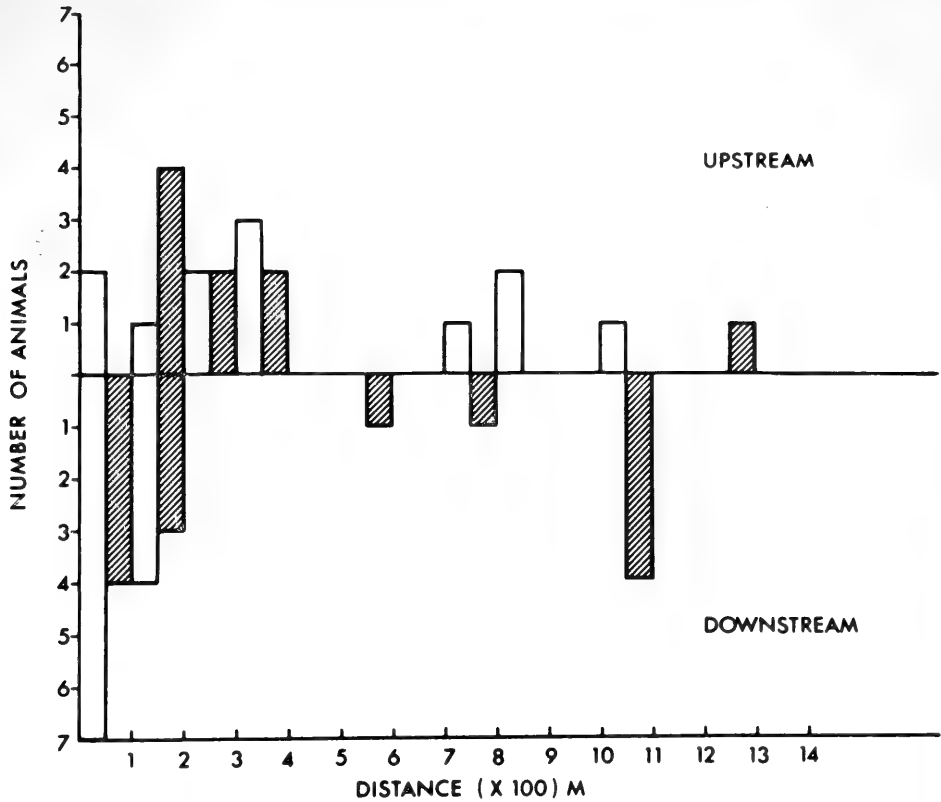


FIG. 4.—Maximum distances moved by marked platypus in the study area. Open bars represent winters 1973 and 1974; striped bars represent summers 1974 and 1975.

few platypus marked up until 1977 in the main part of the study area were captured outside these two pools, regardless of extensive netting operations of May and December of that year (222 net hours). Four animals were found to have moved out of the area to pools upstream, one was found to have moved to a pool 2.6 kilometres downstream, and another was caught early in 1978 in the adjoining creek (some 2.4 kilometres from its point of release six months earlier). In Fig. 5 the numbers of both male and female platypus caught at each trap site are shown, along with a graph indicating the numbers of animals moving to trap sites other than the one at which they were marked. It can be seen from this figure that movements were restricted, especially between the two pools of the main study area (trap sites 6 and 7) and trap sites upstream and downstream from them.

Platypus which were recaptured outside the area in which they were trapped moved reasonable distances in relatively short times. Recapturing of animals at

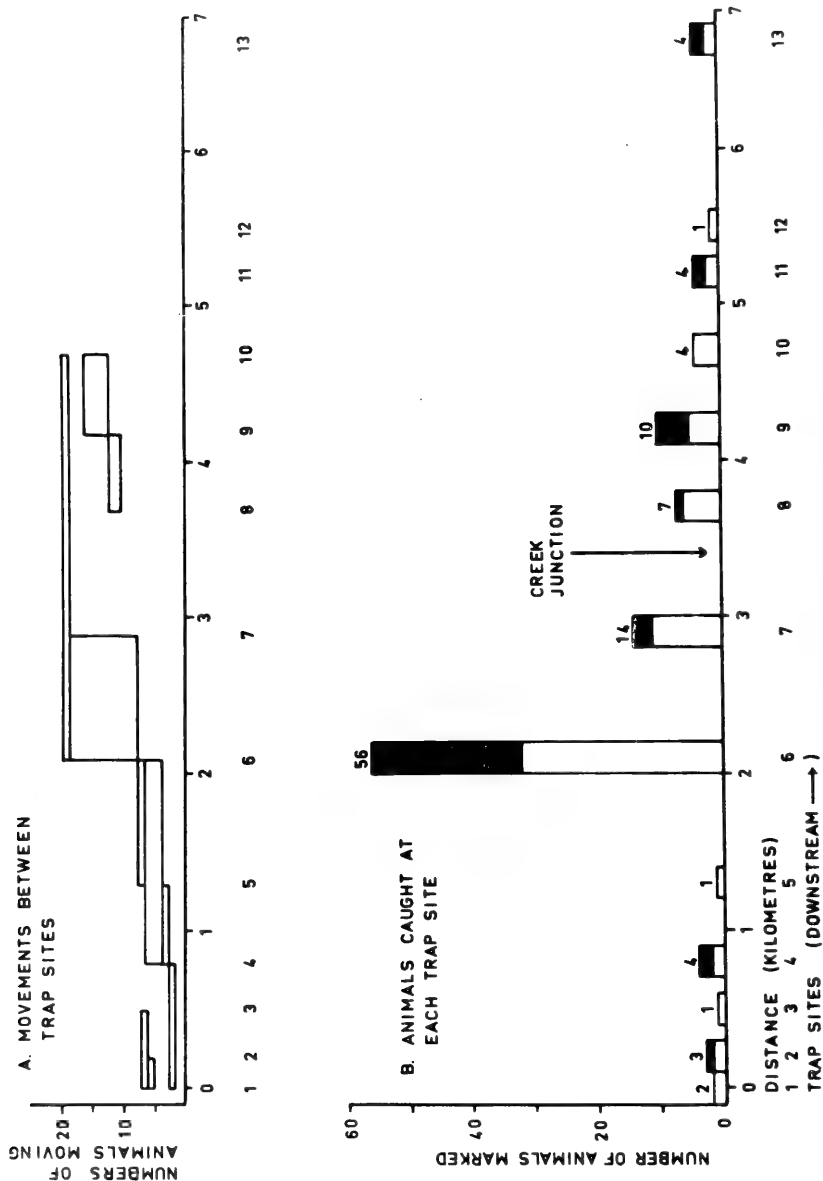


FIG. 5.—Number of platypus marked at each trap-site and distances moved by marked animals between sites. In A the thickness of the horizontal bars indicates the number of individuals moving between trap-sites (the site numbers and distance apart are shown on the horizontal scale for both A and B). In B solid bars represent males and open bars represent females; the numbers at the top of each histogram are total numbers of platypus caught at the site.

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sites over 1 kilometre apart, with only several days between trap nights, occurred several times. For example, one female was caught and marked at trap site 6 on the 30th March, 1976. She was next caught at trap site 4 on the 1st December, 1977, and then recaptured back at trap site 6, a distance of 1.3 kilometres, only five days later. It is, therefore, possible that some animals are more free-ranging than others. The relatively sedentary nature of many of the animals is further indicated, however, by the fact that 57% of all the platypus marked in the area have been recaptured over the study period at least once, and 26% have been recaptured more than once. One female at trap site 6 was caught no less than 10 times after she was first marked in July, 1973!

An interesting sideline to this information is that even floods did not seem to cause displacement of some platypus from the main part of the study area. During the study period three major floods (river levels over the normal banks in the study area), and four floods which reached high up the river banks, passed through the area. The largest, in August, 1974, represented a 10-fold rise in normal river level (Fig. 6). Platypus marked before these floods came through the area were recaptured in subsequent months. In 1977 the main part of the study area was trapped on the nights of the 15th, 16th and 17th of February before a 6.4 metre flood (eight times the minimum level for that year). The area was netted again in March (three weeks after the flood peak), and of the eight platypus caught, five were recaptures, two of which were last caught immediately before the flood. In Fig. 6 the numbers of platypus caught and recaptured in the two main pools at each sampling period throughout the study are shown. The times and levels of the floods passing through the area during this time are also shown.

POPULATION SIZE

The size of the population of platypus in the main part of the study area was determined at each trapping period firstly by calculating the number known to be alive at each point in time. Those known to be alive consisted of those caught at each trapping period plus those marked earlier which were caught during any later trapping period. In late 1976 and in 1977 the pools in the main part of the study area were trapped regularly on a bi-monthly basis, and this data was also used to calculate the population size at each sample-time using the Jolly-Seber Method described by Caughley (1977). This is a stochastic method allowing for immigration and emigration which occurred in the study population. Trapping studies (see above) showed that some platypus moved in and out of the main pools. Further evidence of migration into and out of the area was seen, as there were a number of platypus which were marked at various stages of the study and were never recaptured. There was no evidence that they lost their stainless-steel bands, and as platypus are known to be long-lived (Grant, et al., 1977) it was assumed that these animals had moved out of the area. The Jolly-Seber Method allowed the calculation of the population at each period

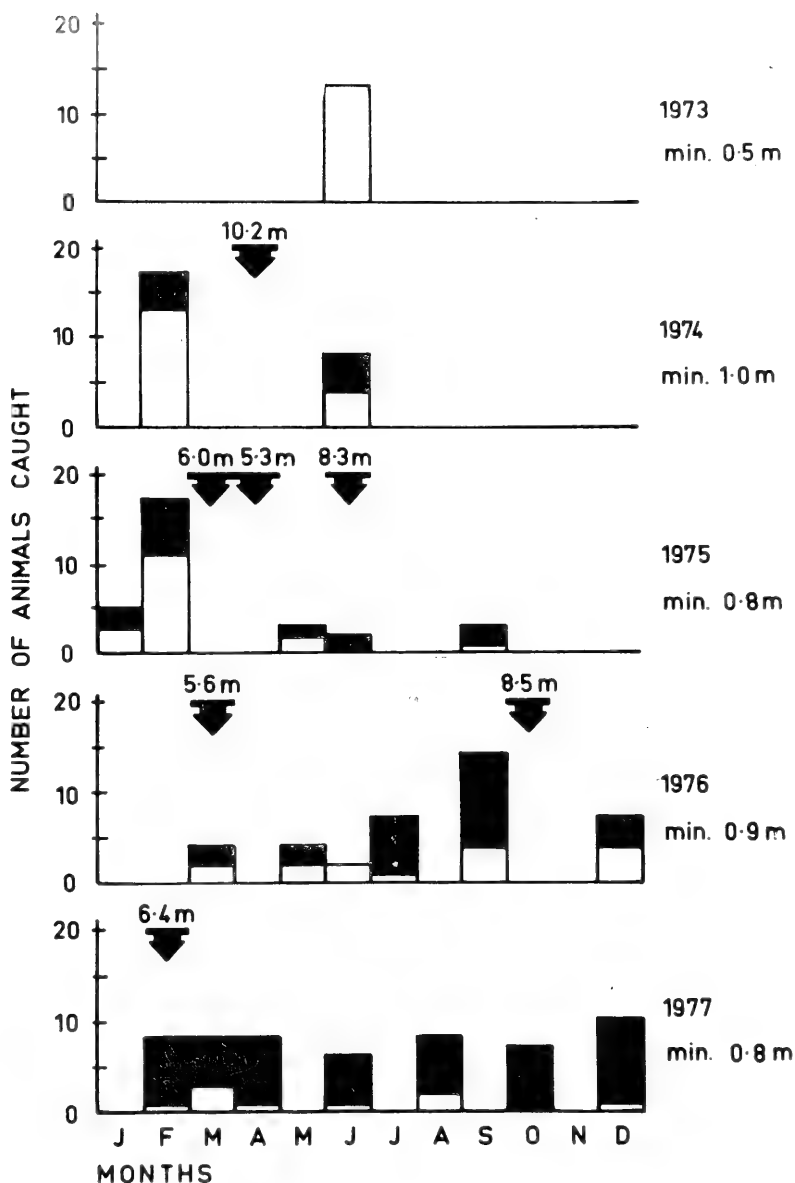


FIG. 6.—Numbers of animals caught and recaptured at each trapping period throughout the study in the two main pools. Flood times and maximum heights (m) are shown as arrows. Histograms represent total captures, including recaptures indicated by the shaded portions.

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except the first and last. Data for males and females were calculated separately in case of differential trapability of the sexes. In two instances the number of male platypus could not be calculated because values of 0 for some of the parameters used in the calculations were obtained. The population estimates for the main two pools of the study area are presented in Table 2 for individual trapping periods.

TABLE 2
POPULATION ESTIMATES

Sample	male	Minimum* female	total	male	Jolly-Seber female	total
1	1	12	13	-	-	-
2	5	13	18	-	-	-
3	0	12	12	-	-	-
4	1	8	9	-	-	-
5	6	12	18	-	-	-
6	1	9	10	-	-	-
7	0	8	8	-	-	-
8	0	9	9	-	-	-
9	1	9	10	-	-	-
10	1	11	12	-	-	-
11	2	12	14	-	-	-
12	3	13	15	-	-	-
13	3	13	16	-	-	-
14	6	12	18	-	-	-
15	7	12	19	8	12	20
16	9	14	23	-	-	-
17	7	13	20	6	14	20
18	7	13	20	x	25	25
19	6	11	17	x	12	12
20	4	8	12	5	9	14
21	3	7	10	-	-	-
mean	3.48	10.95	14.43	6.33	14.40	18.00
s.d.	2.80	2.09	4.38	1.53	6.19	3.46

* Minimum values are those known to be alive. The Jolly-Seber technique was used to estimate the total population.

s.d. = standard deviation; a dash (-) indicates that the total population estimate was not made, while (x) indicates total population estimates could not be made with available data.

The mean estimates for the population at any one time using the two methods were not widely different, being 14 ± 4 platypus known to be alive and 18 ± 4 as a total estimate by the Jolly-Seber method. It should be noted that the first method gives a MINIMUM estimate of the population size, and so a mean population estimate of 18 may be quite acceptable. It must also be noted, however, that the standard errors of the Jolly-Seber estimates at each sampling period were very high (38-80% of the estimated value). A minimum population of between eight and 23 platypus probably occupy the two pools of the main study area. The actual population is likely to be higher than this. A sex ratio

as high as 12 females to one male known to be alive at a particular time suggests that males are less catchable in these pools. The sex ratio for the whole area was found to be 1:1.4 in favour of females (when the juveniles caught in the adjoining creek are considered). A population estimate as different from this as a 1:12 ratio indicates the underestimation of the male population on a "known to be alive" basis. A sex ratio of 1:1 has been found for platypus in other areas of New South Wales and the Australian Capital Territory (Griffiths, pers. comm.). This further suggests differential catchability of the sexes in the study area.

DISCUSSION

Hart (1971) stated, with reference to rodents, that "when food is restricted in cold environments, energy stores are utilised and various behavioural and metabolic changes take place". Seasonal changes in body weight and fat storage have been noted to occur in a variety of mammals (Aleksiuk, 1970, Aleksiuk and Cowan, 1969, and Gilmore, 1969), including the platypus (Temple-Smith, 1973). Temple-Smith noted a decrease of the mean weight of platypus caught in late winter in males (minimum weight 1,300 g. in August-September), and in non-lactating females in spring (minimum weight 910 g. in October-November). Depletion of tail fat storage (as measured by tail volume) was found to parallel the decrease in body weight in the platypus studied by Temple-Smith, who attributed these trends to the possible reduction of availability of food organisms in the colder water temperatures of winter and to the increased metabolic demands on the platypus swimming in the colder water.

The changes in body weights and fat reserves observed in the present study were slightly different from those found by Temple-Smith (1973), although the trends were similar (Figs. 1 and 2). Minimum weights in the platypus from the Shoalhaven River were recorded in the mid-winter months in all animals caught for the first time, and in those recaptured. During the feeding studies (Faragher, et al., 1979) no noticeable decreases in the numbers of benthic organisms from the area were observed in winter samples. These samples were not strictly quantitative, but studies of other eastern Australian rivers and streams (Lake, 1957) also suggest that the secondary productivity of platypus streams may not be low during the months when platypus weights are declining.

The over-wintering behaviour of some of the food species may make the food available to the platypus more time consuming to collect. In Lake Eucumbene, in the Snowy Mountain area of New South Wales, the nymphs of the dragon-fly *Hemicordulia tau* are present in winter in benthic samples, but a much larger proportion of smaller instars are found (Faragher, pers. comm.). The possibility exists that the platypus would find it more time consuming to collect the smaller instars in winter, especially as the lower water temperatures at this time would exert a greater metabolic demand on the platypus (see below). It is interesting to note that in Table 1 the Odonata are not represented as dominant constituents

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of the platypus diet in the winter samples, while they are present in all other seasons.

It would seem that Temple-Smith's suggestion of the reduction in availability of food being an important factor in the weight and fat reserve reductions seen in the platypus in late winter or spring is open to debate. That the environment exerts a much higher metabolic stress on the platypus in the colder months of the year is undeniably a factor which could lead to decline in condition of animals in those months as fat storage areas are mobilised to meet the increased metabolic demand involved in the platypus maintaining its homeothermy. In the study area the winter deep-water temperatures fell as low as 5°C and rose to around 20°C in summer (Fig. 2). The increase in metabolism necessary to cope with this added thermal stress in the species is 18% (Grant and Dawson, 1978 b). Faragher, et al. (1978) have calculated that a 1,500 g. male platypus must daily collect 15 g. more mixed insect food in winter than in summer conditions, assuming it spends 16 hours in the burrow and eight hours in the water. If the animal was forced to spend more time in water to gather this extra food there would be a further increase in metabolic demand. Such increase in metabolic demand would lead to depletion of the stores of energy in fat deposits of the body until the stresses were lifted, and excess food could be consumed to replace the depleted fat reserves. In the platypus this rise in body weight and replacement of tail fat coincide with the late spring elevation of water temperature in the study area (Fig. 2).

The fur of the platypus is quite short, but is very dense. It consists of a layer of woolly underfur, overlain by blade-like guard hairs. The fur traps a layer of air in the kinks of the fibres of the underfur and between the underfur and blades of the guard hairs. At air temperatures below 15°C vascular adjustments make the most significant contribution to the insulation of the body of the platypus, but above this temperature the fur provides 50-90% of the total insulation of the body. In water the insulation of the fur of the species is 30-40% of its value in air, but still traps a layer of air and adds to the insulation of the body (Grant and Dawson, 1978 b). Both dorsal and ventral pelage were moulted throughout the year in the platypus in the study area, but heavy moulting of dorsal fur occurred only in the late spring and summer months, when water temperatures were relatively high (Fig. 3). Air temperatures in these months seldom fell below 10°C, and the underground temperature was around 18°C (Grant and Dawson, 1978 b). By comparison, in the winter months, when only light or moderate moult occurred, air temperatures frequently fell below freezing at night. Ventral fur appeared to be moulted very gradually with the incidence of pelage, with more than light moult showing being infrequent. Ryder and Kay (1973) indicated that asynchronous activity of hair follicles and slow loss and replacement of hairs can give the fur of an animal the appearance of not moulting at all. Such a mechanism allows the animal to maintain maximum fur insulation, while still replacing worn-out hair.

Temple-Smith (1973) recorded many more platypus in "heavy" moult than were found in this study. He found the peak moult to be in late winter and spring in both males and non-lactating female. Unlike the Shoalhaven River platypus, Temple-Smith's animals (Murrumbidgee River) had completed their moult by December or early January, except in the case of lactating females whose moult continued into April. Females were not separated into lactating and non-lactating in the present study until late in 1977, when lactation was detected by milk let-down after injection of oxytocin. However, out of five females found to be definitely lactating in December, 1977, only one animal showed more than light moult. It would seem that the platypus, at least in the Shoalhaven River, restrict their moulting patterns in the colder months of the year to gradual replacement of fur. This would maximise the insulation of the pelage at this time of added thermal stress. Heavily moulted furs of the platypus have insulation values in air which are significantly ($p < 0.05$) lower than the values measured on pelts with no moult or light moult (Grant and Dawson, 1978 b).

The platypus can be described as an "opportunistic carnivore" (Faragher, et al., 1979), eating mainly insect larvae (Table 1). The prey groups eaten include consumers from several levels of the lotic food web. The Odonata are all active predators, as are the Megaloptera and frogs. The dipteran and trichopteran constituents of the diet include both herbivores and carnivores (Williams, 1968), and the Decapoda (*Paratya* sp.) species is mainly a detritus feeder (Chapman and Lewis, 1976). The platypus therefore depends on the secondary productivity of the river system for its existence in the lakes, rivers and streams of eastern Australia. The secondary productivity of any inland waterway, specifically the benthic productivity, must determine the number of platypus occurring in that waterway.

The Shoalhaven River study area is not a closed system. It can be affected by the parts of the river upstream and downstream from it, as well as by the adjacent creek. Movement of platypus occurred in and out of the area during the study. The reason for this movement is not evident from the results of the work carried out, but it appears that the main two pools of the study area, with their connecting riffles, support a resident population of at least 14 to 18 individuals (Table 2). Other individual animals move in and out of the area and were occasionally caught while they were in the area. The productivity of the main part of the area is therefore supporting the resident population at all times, as well as a number of these transients.

Very little work has been carried out on the measurement of secondary productivity of Australian rivers. Mann (1975) gives estimates of the secondary productivity of both herbivorous (and detritivorous) and carnivorous invertebrates in an American river, and these can be used to calculate the possible secondary productivity of the study area. Productivity in the two main pools and rapids ($43,600 \text{ m}^2$) could be $139,140 \text{ kJ. day}^{-1}$ for herbivorous (and detritivorous) invertebrates and $18,519 \text{ kJ. day}^{-1}$ for carnivorous forms of benthic fauna. Three

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other values of total secondary productivity in rivers (Waters, 1977) yield estimates for the study area from 8,759 kJ. day⁻¹ to as high as 500,528 kJ. day⁻¹. Table 3 shows the metabolic demands of platypus in the study area in summer and winter, calculated from the data of Grant and Dawson (1978 b) using the lowest mean winter weight and the highest mean summer weight of both males and females, and assuming each animal spends 16 hours in the burrow and eight hours foraging for food in the water each day. Metabolism is measured on a per unit of weight basis, and it is interesting to note that because of the depressed winter weight used in the calculations, the summer and winter metabolic requirements of platypus are almost identical after the initial weight loss. However, the main point illustrated in Table 3 is that the productivity of the benthos of the area is more than adequate to support the resident and transient platypus population.

TABLE 3
ESTIMATED CONSUMPTION OF SECONDARY PRODUCTIVITY OF THE
SHOALHAVEN RIVER STUDY AREA BY THE MAXIMUM NUMBER OF
PLATYPUS KNOWN TO BE ALIVE DURING THE STUDY

	Body Weight (g.)	Metabolic Demand (kJ. day ⁻¹)	Population	Total Metabolic Demand (kJ. day ⁻¹)
<i>Summer</i>				
Females	950	273	14	3822
Males	1600	459	9	4131
				<hr/> 7953
<i>Winter</i>				
Females	735	251	14	3514
Males	1260	430	9	3870
				<hr/> 7384

Allen (1951) showed that flooding markedly reduced both the biomass and the density of certain species (especially species not inhabiting riffle areas) of the benthos of a New Zealand trout stream. Data from the present study showed no significant difference ($p \gg 0.05$) between the weights of platypus caught two and eight weeks after major flooding, and those of animals caught in the same months in years when no flooding occurred in those months. Clearly benthos of the study area is capable of supporting the existing platypus population, even in times of biomass depletion after flooding.

The platypus inhabits most of the waterways of the eastern Australian mainland and Tasmania. It has been found to inhabit sewage-polluted rivers (Griffiths, pers. comm.), as well as clean freshwater streams, rivers and lakes. The species relies for its continued existence on the plentiful supply of benthic fauna in these locations. Platypus compete to some extent with fish, waterfowl and the water rat (*Hydromys chrysogaster*) for this food, due to some overlap in

their diets (Faragher, et al., 1979). However, these species co-exist successfully with each other and with the platypus. It is the intrusion of man into the ecology of the inland waterways of eastern Australian which may become a threat to the continuing presence of the platypus in the faunal composition of the region. Deoxygenation of water due to the bacterial breakdown of excessive sewage outfall, the toxic effects of various chemicals, including insecticides, herbicides and the salts of heavy metals, and the increasing threat of thermal pollution in Australian waterways all have the potential to destroy or radically alter the benthos of these systems (Weatherley, et al., 1967, and Bayly and Williams, 1974). Such occurrences could eliminate or dramatically reduce the food species available to meet the metabolic demands of *Ornithorhynchus anatinus*.

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The Role of the Excurrent Ducts from the Testes of Testicond Mammals

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ABSTRACT

The male reproductive tract of monotremes and other testicond mammals is of particular interest, since the testes are located in the primitive position, within the abdominal cavity. The epididymis courses caudally from the testis under the dorsal wall of the abdominal cavity, rather than folding around the testis to form a head, body and tail as in scrotal mammals. Nevertheless, the epididymis of testicond mammals is anatomically differentiated. There is a wide proximal region (incorporating the efferent ducts) which courses over the testis, a narrower distal region caudal to the testis and (usually) a narrower isthmus joining the two regions.

Histologically the epididymis is divided into an initial and terminal segment which roughly corresponds to the proximal region, and the isthmus and distal regions of the epididymis respectively.

The functions of the different parts of the excurrent ducts of testicond mammals are much the same as in scrotal mammals. The most noteworthy feature is the development of the distal region, which stores spermatozoa accessible for ejaculation. Relative to the animal's size (the echidna and elephant have been studied to date) this region does not store as many spermatozoa as the analogous region in scrotal mammals (tail of the epididymis). Consequently, at any particular time, fewer spermatozoa are available for ejaculation. Further, the location of the storage region varies between the different testicond mammals from just adjacent to the testis (echidna) to the caudal end of the abdominal cavity just below the tail (elephant shrew). The significance of these adaptations is discussed.

INTRODUCTION

The evolution of the excurrent ducts from the mammalian testis has received relatively little attention. Benoit (1926) studied a number of scrotal mammals and described considerable variation in the anatomy of the vasa efferentia. However, he concluded that in the epididymal duct of all species that he examined there was an "initial segment" which was characterised by a high columnar epithelium and a lumen containing a low concentration of spermatozoa. Subsequently, a number of workers further classified the structural differentiation of the epididymis of scrotal mammals (e.g. Reid & Cleland, 1957), and these reports have recently been reviewed and summarised for comparative purposes by Glover and Nicander (Glover & Nicander, 1971; Nicander & Glover, 1973). Glover also studied the

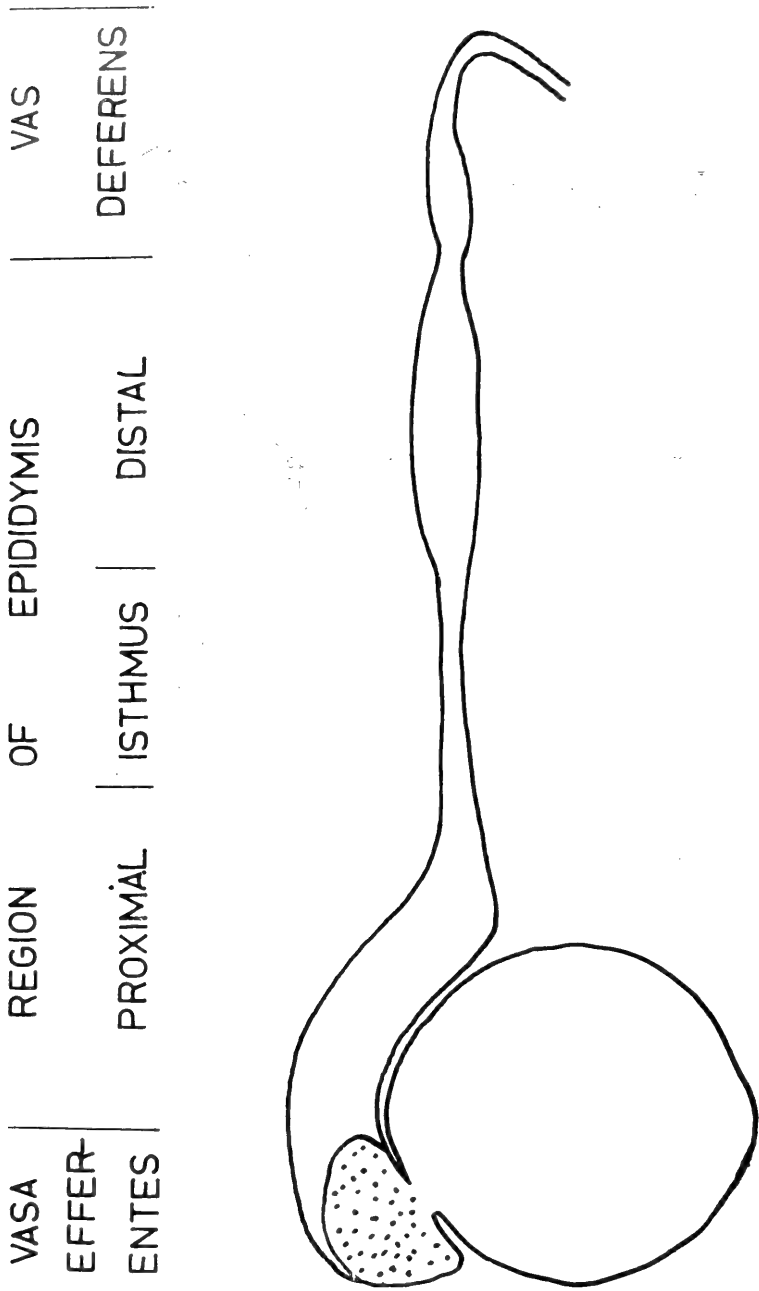


FIG. 1.—Generalised anatomy of the testis and excurrent ducts of testicond mammals. The efferent ducts (spotted area) leave the rete testis at about the dorsal pole of the testis and join the epididymis, which courses caudally under the dorsal wall of the abdominal cavity.

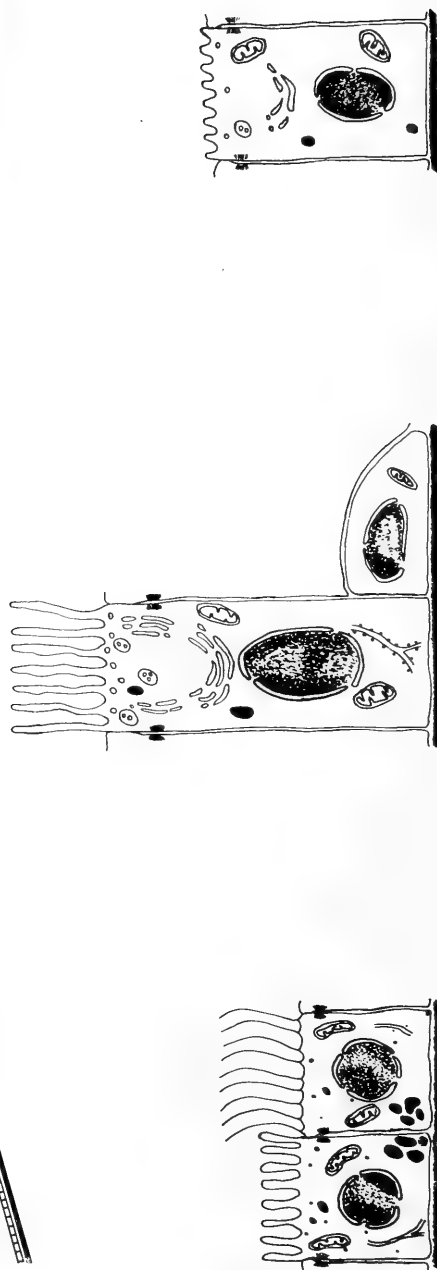
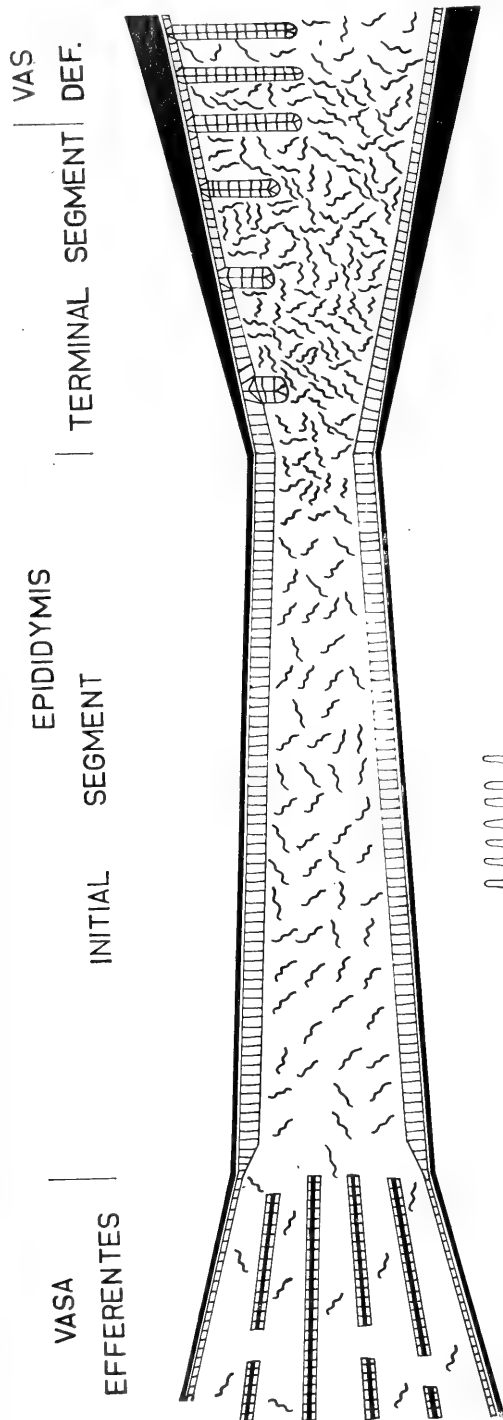
epididymis of some of the mammals with undescended testes (the testicond mammals) and suggested that this organ may have been the prime mover in the evolutionary descent of the mammalian testis into the scrotum. The proposal was later supported by Bedford (1977), who noted some adaptive advantages of a scrotal epididymis. However, there have been no detailed studies of the structure and function of the excurrent ducts of the testes of testicond mammals and the relationship of the epididymis of testicond and scrotal mammals is unresolved (Glover, 1968; Hanks, 1977; Jones, Rowlands & Skinner, 1974; Short, Mann & Hays, 1967). As much of the contention about the testicond epididymis concerned the elephant epididymis, the structure and function of this was studied initially. The purpose of this report is to review what is known of the structure and function of the excurrent ducts of the testicond testis and to draw attention to some findings relating to the evolution of the epididymis.

The review is based on our studies of the structure, cytochemistry and function of the elephant (*Loxodonta africana*) reproductive tract, the anatomy and histology of the echidna (*Tachyglossus aculeatus*) reproductive tract and the anatomy of the elephant shrew (*Macroscelides spp.* and *Elephantulus spp.*) reproductive tract, and reports (Glover & Sale, 1968; Temple-Smith, 1973) of studies on the rock hyrax (*Procavia spp.* and *Heterohyrax spp.*) and the platypus (*Ornithorhynchus anatinus*).

ANATOMY

The testes of testicond mammals lie beside or just caudal to the kidneys. They are suspended from the dorsal wall of the abdominal cavity by a peritoneal fold. The efferent ducts leave the rete testis on the dorsal surface of the testes and join the epididymis, which (supported by a peritoneal fold) traverses caudally below the dorsal wall of the abdominal cavity.

Fig. 1 shows a generalised diagram of the testicond testis and accessory ducts. In the elephant the efferent ducts radiate from the testis, and each duct separately joins the epididymis at right angles. Each duct is highly convoluted and enmeshed in connective tissue so that anatomically it appears as a cord which consists of a wide proximal region which courses over the surface of the testis, a narrower distal region located caudal to the testis and an even narrower isthmus which joins the two wider regions of the epididymis. The length and width of the isthmus varies considerably. It is recognised as little more than a fold in the epididymal cord at the point where the epididymis leaves the testis of the echidna, it is more obvious in the platypus and is long in the rock hyrax (Glover & Sale, 1968) and elephant, where generally its length and width depend upon the size of the animal. However, in the elephant shrew the isthmus is long and narrows to an unconvoluted duct which passes below the bladder to the distal region of the epididymis, which is located just below the rectum at the most posterior end of the abdominal cavity. The distal region of the elephant shrew epididymis is more distinct than in the other species which have been studied, and only a short



unconvoluted vas deferens joins it to the urogenital sinus. In the testicond mammals, other than the elephant shrew, the vas deferens is convoluted and, consequently, relatively long, and there is no clear demarkation where the epididymis ends and the vas deferens begins.

The anatomical differentiation of the epididymis of testicond mammals into three regions is strikingly similar to the differentiation of the epididymis of scrotal mammals into a head, body and tail, except that in the latter the epididymis is folded on the dorsal and ventral poles of the testis and the tail of the epididymis appears larger than in testicond mammals. It is tempting to suggest that the analogous regions of the epididymis of these two groups of mammals have similar functions and that the anatomy of the epididymis is related to these functions. Such a suggestion is based on the consideration that the overall dimensions of the three regions are determined by such factors as duct diameter and length, and the vasculature of the ducts (Kormano, Suoranta & Reijonen, 1973; Kormano & Reijonen, 1976; Setchell, Waites & Till, 1964). However, there is not much evidence to support this proposal. Indeed, Glover (1974) concluded that there is little correlation between the function and the anatomy of the scrotal epididymis.

HISTOLOGY AND CYTOLOGY

The structure of the excurrent ducts of a testicond testis is shown schematically in Fig. 2. The efferent ducts are adapted to expose a large surface of epithelium to the luminal contents. They are long, narrow, lined by a simple cuboidal or low columnar epithelium, and contain few spermatozoa in the lumen. The lining epithelium carries either cilia or low microvilli. The cells are characterised by round, centrally located nuclei, numerous mitochondria, and ribosomes and aggregates of electron dense material which, in the elephant, was histochemically identified as lipofuscin.

In general the epididymis is lined by a pseudostratified, stereociliated columnar epithelium with a composition of cells similar to that found in scrotal mammals (Reid & Cleland, 1957), i.e. principal, basal, halo and "clear" cells. There are two histologically distinct segments of the epididymis, an initial and terminal segment (Table 1 and Fig. 2). The initial segment is similar to that described in scrotal mammals by Benoit (1926). It roughly corresponds to the anatomically distinct proximal region of the epididymis. It is characterized by a high epithelium long stereocilia and a moderate concentration of spermatozoa in the lumen. The nuclei are elongate in the principal cells, and basal cells are more frequent than in the terminal segment. In the elephant, at least, there is a change in the character-

FIG. 2.—Schematic diagram of the excurrent ducts of the testis of testicond mammals and details (below) of the lining epithelium. The shaded area indicates the periductal layer of smooth muscle, the vertical striations indicate the lining epithelium (and epithelial folds in the terminal segment of the epididymis and the vas deferens), and the wriggly lines indicate spermatozoa in the lumen.

istics of the duct from the proximal to the distal end of the segment. This involves an increase in epithelial height, stereocilia length and sperm concentration (all species), and a decrease in duct and lumen diameter. Indeed, the concentration of spermatozoa in the distal end of the initial segment is greater than elsewhere in the duct. Cytological studies (of the elephant) indicate that the supranuclear cytoplasm of the principal cells has extensively developed Golgi apparatus, and is also characterised by multivesicular bodies, tertiary lysosomes and apical pinocytotic vesicles. The occurrence of the multivesicular bodies and lipid is generally greater towards the distal end of the segment.

The terminal segment of the epididymis is characterised by a wide lumen packed with spermatozoa, a low lining epithelium containing oval nuclei, and a periductal smooth muscle layer which increases in thickness along the length of the epididymal duct and vas deferens. The dimensional changes between the initial and terminal segments occur in the isthmus of the epididymis, and there is little variation in the histology of the epithelium in the distal region. In the elephant the epithelium lining the distal region is a pseudostratified columnar type with short stereocilia. In the echidna it is a low columnar type with a few basal cells present, but no discernible microvilli, even in thick Araldite sections. However, reports on the rock hyrax (Glover & Sale, 1968) and platypus (Temple-Smith, 1973) indicate that the terminal segment is lined by a simple cuboidal epithelium. The cytology of the epithelium in the distal segment appears to be qualitatively similar to the initial segment; however, generally there are fewer organelles present. In the elephant and echidna the terminal segment is characterised by epithelial folds (villi, Fig. 3), which extend into the lumen (in the elephant they are also present in the proximal part of the initial segment). These are well vascularised and increase in length and frequency along the epididymal duct and vas deferens. They have not been described in the rock hyrax or platypus, although it is noteworthy that Temple-Smith (1973) described the ducts in the terminal segment of the platypus epididymis as being "irregular-shaped tubules".

It is concluded that the structure of the initial and terminal segments of the epididymis of the testicond mammals is in accord with the proposal made by Glover and Nicander (Glover & Nicander, 1971; Nicander & Glover, 1973). However, the middle segment described by these workers is not as obvious as in the scrotal mammals. A similar region to that described by Glover and Nicander can be recognised as a transitional zone between the initial and terminal segment; mainly the caudal end of the initial segment. It is characterised as the region where spermatozoa become more concentrated than elsewhere in the duct and where changes associated with sperm maturation occur (i.e. migration of the cytoplasmic droplet in the spermatozoa of the elephant and rock hyrax and development of a regular clumping of spermatozoa in the monotremes). However, the histological characteristics of the middle segment which were described by Glover and Nicander are not regularly obvious in the testicond mammals. Some increased cellular vacuolation and a decrease in stereocilia height may be recognised

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in the elephant, but this does not occur in the echidna and has not been recorded for the other testicond mammals which have been examined.

FUNCTION

It is suggested that the functions of the accessory ducts of the testis involve some division of labour along their length, and these functions are related to their structure (Table 1). The functions are much the same as has been described in scrotal mammals (Crabo, 1965; Levine and Marsh, 1971). Most of the fluid leaving the testis is reabsorbed in the efferent ducts. This is demonstrated by spermatozoa of luminal fluids collected from the ducts of recently slaughtered elephants. They indicate that about 95% of the testicular fluid has been reabsorbed when spermatozoa reach the most proximal part of the initial segment. Estimates of sperm concentrations in homogenates of efferent ducts and the proximal region of the echidna epididymis (Table 2) also support this conclusion. The efferent ducts are adapted for a reabsorptive function in that they are numerous (up to 20 in the elephant), highly convoluted, long and narrow, and are lined by a low

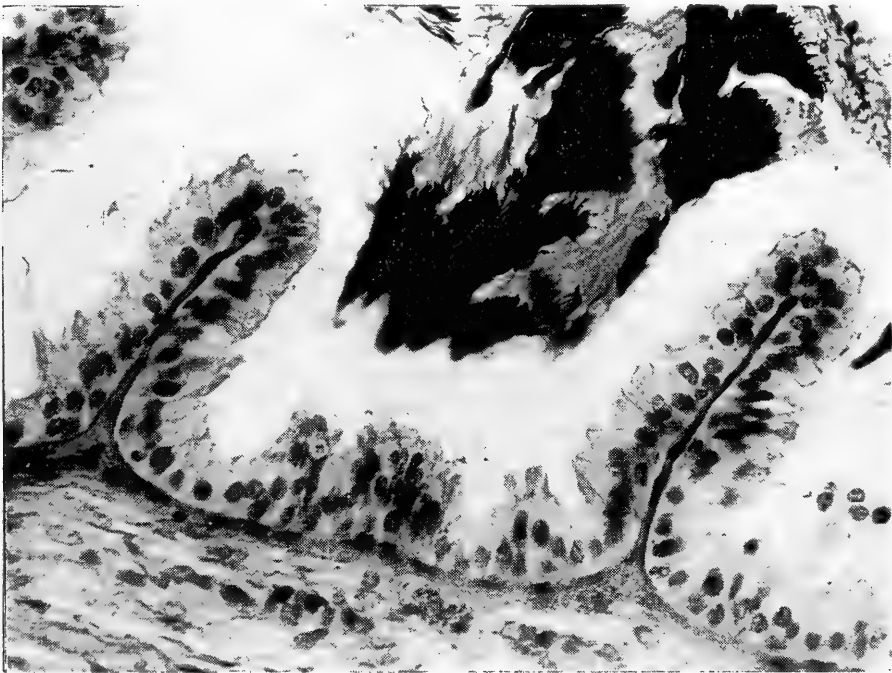


FIG. 3.—Section of the duct in the terminal segment of the epididymis of the echidna showing the epithelial folds and the clumping of sperm in the duct lumen. Paraffin section, H and E x 5,000.

epithelium. Biochemical determinations of the elephant luminal fluids indicate that some protein must be reabsorbed, as well as the fluid from the efferent ducts.

TABLE 1

SUGGESTED FUNCTIONS* OF THE EXCURRENT DUCTS FROM
THE TESTIS OF TESTICOND MAMMALS AND CLASSIFICATION
ACCORDING TO ANATOMY AND TISSUE STRUCTURE

ANATOMICAL DIFFERENTIATION		VASA EFFERENTIA	EPIDIDYMIS		
			Proximal	Isthmus	Distal
TISSUE DIFFERENTIATION			Initial	Terminal	
EPITHELIUM:	Absorptive	++	+	—	—
	Secretory	—	++	+	+
SPERM:	Concentration	++	+	—	—
	Maturation	—	—	← ++ →	—
	Storage	—	—	—	++

*The relative amount of activity is indicated by the number of + signs.

The elephant studies also indicate that the initial segment of the epididymis is involved in the reabsorption of fluid (about 50% of the fluid entering the epididymis) and protein. This finding is confirmed (Table 2) by determinations of sperm concentrations in homogenates of the echidna epididymis. The considerable length of the epididymal duct and the long epithelial stereocilia in this region would provide a large surface for the reabsorption of fluid. The presence of extensive epithelial folds in the initial segment of the elephant epididymis also provides an adaptation for this purpose. The considerable height of the epithelium in this segment probably reflects the synthetic activity of the epithelium, e.g. the production of protein, mucosubstances and glycerophosphorylcholine.

The magnitude of spermatocrits of luminal fluids from the elephant epididymis decrease by about 10% in the isthmus region, indicating that it is involved in some secretory activity. However, considering the virtual absence of an isthmus in the echidna epididymis and the absence of convolutions over a considerable length of the isthmus in the elephant shrew epididymis, it is probable that in some species this region may mainly act as a connection between the proximal and distal regions of the epididymis.

It is suggested that the distal region of the epididymis is adapted for the storage of spermatozoa ready for ejaculation. Thus the region contains a greater number of spermatozoa per gram of tissue than more proximal regions (Table 2), it is well vascularised (particularly in species containing epithelial folds) and the low epithelium would provide a low resistance to the diffusion of gases between the blood capillaries and the duct lumen. The thick layer of periductal muscle makes the spermatozoa in this region most accessible during ejaculation, and this

EPIDIDYMIS OF TESTICOND MAMMALS

accessibility is undoubtedly a reason why the region has developed closer to the urinogenital sinus than the testis, i.e. a reason for the development of an isthmus. Indeed the location of the storage region of the elephant shrew epididymis minimises the distance that sperm must travel during ejaculation. However, its position just below the skin at the base of the tail also supports the suggestion by Glover (1968) and Bedford (1977) that there may be an adaptive advantage in being able to differentially modify its thermoregulation compared to other parts of the epididymis.

TABLE 2

DISTRIBUTION OF SPERMATOZOA IN THE EXCURRENT DUCTS OF THE TESTIS OF TESTICOND AND SCROTAL MAMMALS

ANIMAL	SPERM	VASA EFFER- ENTES	EPIDIDYMIS			VAS DEF- ERENS	STAND- ARD ERROR
			PROXIMAL	ISTHMUS	DISTAL		
RABBIT ¹	No. ⁴	—	300	116	1,388	96	74
	%	—	16	6	73	5	—
RAM ²	No.	—	17,300	8,400	104,300	1,500	—
	%	—	13	6	79	1	—
ECHIDNA ³	No.	2.8	1,146	—	395	44	289
	%	0.0	72	—	25	3	—
	No sperm/gm	30	186	—	440	135	101
ELEPHANT ³	No.	—	40,270	13,382	29,869	4,059	8,181
	%	—	46	15	34	5	—
	No sperm/gm	—	96	161	262	47	57

¹, Orgebin-Crist (1968); ², Chang (1945); ³, means of two replicates (animals);

⁴, number of spermatozoa per animal x 10⁶.

Probably the most noteworthy feature of the epididymis of testicond mammals is that, although for their body weight these animals contain about as many extragonadal spermatozoa as scrotal mammals (Jones, Rowlands & Skinner, 1974; Jones, unpublished date), the distal (storage) region of the testicond epididymis contains a smaller proportion of the total number of epididymal spermatozoa than the analogous region in scrotal mammals (Table 2). Consequently, the testicond mammals may be limited in the number of spermatozoa that they can ejaculate within a relatively short period. Further studies are required to assess the relationship between this finding and the rate of sperm production and transport in the male, the efficiency of insemination and transport of spermatozoa in the female reproductive tract and the reproductive ethology of the testicond mammals.

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Reproduction in Male Monotremes

F. N. CARRICK and R. L. HUGHES

The study of the reproductive biology of the monotremes has always been dominated by the phenomenon of oviparity, with a particular fascination for discerning the processes that lead to the hatching of a young mammal from an incubated egg. This has reinforced the trend seen in other mammalian groups for research in male reproduction to be less fashionable (Setchell, 1977). However, some reproductive characteristics of male monotremes are as different from those of other mammals as is oviparity in the case of the female. The review that follows will largely be concerned with the distinctive features of reproduction in male monotremes, with more emphasis being given to recently studied phenomena.

The literature of the nineteenth and early twentieth centuries was primarily concerned with descriptions of the gross anatomy of the reproductive system. However Retzius (1906) described the monotreme spermatozoon, and Benda (1906) reported on the cell types present in the germinal epithelium of the testes of both *Ornithorhynchus* and *Tachyglossus*. The earlier literature on reproduction in male monotremes has been reviewed by Griffiths (1968) and Temple-Smith (1973).

GROSS ANATOMY OF THE MALE REPRODUCTIVE TRACT

Figure 1 indicates the simplicity of the genital tracts of male monotremes in comparison with those of male marsupials and eutherians (see Rodger & Hughes, 1973). The testes lie within the abdominal cavity, situated just caudo-dorsal to the kidneys. The bulk of the disproportionately large epididymides lies further caudad, and they are not as intimately associated in topographic position with the testes as is usually found in scrotal mammals. The ductus deferentia are not recurrent and join the urethra just cranial to the ureters.

There are no ampullae, seminal vesicles, coagulating glands or discrete prostate glands as have been described for many eutherians. The markedly enlarged disseminate prostate and complex array of bulbourethral glands, described for many marsupials, are also lacking. However, an inconspicuous development of disseminate glandular tissue is present surrounding the cranial portion of the urethra, and a single pair of well developed bulbourethral glands communicates with the more caudal region of the urethra via elongated ducts. The urethra terminates in a large penis, which in the two Australian genera is of fairly elaborate form.

BREEDING SEASONAL CHANGES IN THE MONOTREME TESTIS

Fragmentary observations on the platypus by Bennett (1835, 1859) and Burrell (1927) led them to suggest the occurrence of seasonality in testicular activity. However this was not confirmed histologically, and the small sample size, restricted locality, timing of the sample and the ageing criteria employed were all criticised by Temple-Smith (1973). Detailed information on seasonal changes in the testis of the platypus based on a much more extensive series of specimens has been provided by Temple-Smith (1973). Griffiths and Elliott (pers. comm) have also observed a seasonal cycle of the testis in *Ornithorhynchus* and *Tachyglossus*, and they have made more limited observations in *Zaglossus* as well. Our own observations were incidental to ultrastructural and endocrinological studies, and they also confirm the occurrence of an annual cycle of involution and recrudescence of the testis of the platypus.

It can be deduced from all these observations that the testis reaches its maximum activity in spring. This is evidenced by the large size (up to about 16 g/kg) and the histological, histochemical and ultra-structural appearance of the seminiferous epithelium and interstitial tissue. A marked involution then follows and results in minimal testis weights (about 1 g/kg), absence of spermatozoa or spermatogenesis and regression of the Leydig cells. The involution lasts throughout summer and early autumn, until recrudescence begins in late autumn/early winter.

Temple-Smith (1973) concludes that the pre-nuptual spermatogenesis seen in the platypus indicates greater affinity with the seasonal breeding pattern of other mammals (and birds), rather than with the pattern of post-nuptual spermatogenesis seen in reptiles. The seasonal cycle of the interstitial tissue was also considered by Temple-Smith (1973) to indicate a basically mammalian pattern, although some features of the lipid cycle and invasion by phagocytic cells were considered to be attenuated versions of phenomena more commonly seen in reptiles and birds. However, Temple-Smith indicated that caution should be exercised in suggesting that physiological and phylogenetical intermediacy were synonymous.

ACCESSORY SEX GLANDS

PROSTATE

MacKenzie and Owen (1919) do not mention prostatic tissue in the genital tract of the monotremes. This probably reflects a common misinterpretation of Oudemans (1892), who reported that the monotremes lacked a *discrete* prostate. However, as noted by Temple-Smith (1973), Oudemans did in fact describe disseminate urethral glands and indicated that these accounted for the visible thickening of the urethra of the male platypus near its junction with the bladder, as was previously described by Saint-Hilaire (1827).

Temple-Smith (1973) studied the histology and histochemistry of these glands. He found no regional differentiation of the prostate gland, as was reported for marsupials (Rodger & Hughes, 1973), and his histochemical studies indicated

that the major secretory product of this gland was probably a sialic acid-rich mucoprotein. However, histochemically demonstrable intracellular precursors were present in both breeding and non-breeding adults as well as in a juvenile male; although he noted that the juvenile exhibited a lesser degree of glandular development than was seen in the adults. This apparent lack of an obvious seasonal secretory cycle led him to question the semantics of reference to the tissue as either "urethral glands" or a "disseminate prostate". Almost certainly this tissue is homologous with the disseminate prostate of marsupials, and many eutherians possess both a discrete and a disseminate prostate gland.

Our limited ultrastructural observations on the platypus prostate gland indicate the occurrence of secretory activity during the breeding season, but no such observations of this tissue have made, as yet, during the non-breeding season. Such electron-microscopic observations should reveal whether the prostatic secretion is arrested or decreases in platypus with regressed testes. In this context, it is significant that even during the non-breeding season the regressed testes still produce small amounts of testosterone (Carrick, 1977); and, if the prostatic tissue has a low threshold for androgen support, some precursor synthesis may be expected to continue throughout the year. It is apparent that the secretory activity of the prostate gland requires further study.

COWPER'S GLANDS, SCENT GLANDS AND CRURAL SYSTEM

Seasonal changes have been observed in the size and activity of the Cowper's glands, scent glands and crural glands of the platypus by Temple-Smith (1973). The peak activity of the secretory cells of these glands coincided approximately with peak testicular activity, although the initiation of development in these secretory tissues lagged behind that of the seminiferous epithelium of the testis. Since the development of these glands was approximately correlated with the activity of the testicular interstitial tissue, Temple-Smith concluded that they were androgen dependent. The crural glandular system (associated with the poison spur) is the subject of another paper by Temple-Smith elsewhere in this symposium.

The structure of Cowper's glands has been described in the echidna by Voit (1906) and Griffiths (1968) and in the platypus by Temple-Smith (1973). Histochemical tests of the secretory glandular epithelium led Temple-Smith to conclude that the major secretory product was probably an acidic mucopolysaccharide. He further speculated that this viscous mucin emanating from the Cowper's glands of the platypus in the breeding season might possibly be involved in the formation of a 'gel-plug'. However, no data at present exist concerning whether a 'gel-plug' forms following copulation in the platypus.

Little is known concerning the function of the scent glands of the male platypus; however, Temple-Smith's (1973) findings, that the size and the activity of these glands are correlated with the onset of the breeding season as well as the seasonal activity of the testis, would suggest that they are very probably involved in reproductive behaviour.

SPERMATOZOON

Superficially, the filiform morphology of the spermatozoon of the monotremes appears to be uniquely different from the spermatozoa of the viviparous mammals. Therefore, the lack of data on the detailed morphology of the male monotreme gamete is surprising.

Retzius (1906) described the histological appearance of the monotreme spermatozoon, but there are no published accounts of the morphology of the sperm of *Zaglossus*. The only published observations of the ultrastructure of monotreme spermatozoa are the description of the fine structure of the epididymal spermatozoon of *Tachyglossus* by Hughes (in Griffiths, 1968) and some preliminary observations on *Ornithorhynchus* by Carrick (1977).

Recently, further information on the ultrastructure of monotreme sperm has been obtained (Hughes & Carrick, 1978). They noted that some aspects of the fine structure of the sperm of *O. anatinus* and *T. aculeatus* were reminiscent of the sauropsid condition. These features included: the size and arrangement of the axonemal/dense fibre complex in the mid-piece; presence of extracellular tubules in the head region of 'mature' echidna sperm; the occurrence of a spiral fibrous sheath of the principal piece; and the lack of a definitive neck region as well as the overall smoothly tapering spindle shape. However, major differences from the sauropsid condition were also apparent, such as: the lack of juxtamitochondrial dense bodies; the absence of a sub-acrosomal rod; the lack of a major extension of spiral fibrous sheath, beneath the mitochondrial sheath, anterior to the annulus; and the lack of fusion of the fibrous sheath with peripheral dense fibres of the axonemal complex. Although the overall morphology of monotreme sperm was distinctive, the basic ground-plan was considered, in many respects, to be referable to the pattern found in the unspecialised spermatozoa of many Eutheria.

In contrast, metatherian spermatozoa exhibit an extremely divergent morphology (Harding *et al.*, 1977). Griffiths (1968) has also cautioned against excessive emphasis on the "reptilian" character of the spermatozoa of monotremes. He cites Franzen (1956) as pointing out that filiform sperm are found in individuals of many invertebrate phyla, while other members of the same phyla possess considerably less differentiated spermatozoa.

TESTIS

SEMINIFEROUS EPITHELIUM

Spermiogenesis in both *Ornithorhynchus* and *Tachyglossus* was described by Benda (1906). Temple-Smith (1973) discussed the histology of the testis of *Ornithorhynchus*, but this was mainly in the context of a study of seasonal changes in the seminiferous epithelium and interstitial tissue. Griffiths and Elliott (pers. comm.) have made some observations on histological changes in the testes of both *Tachyglossus* and *Zaglossus bruijnii* in relation to the breeding season. Hughes and

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Carrick (1978) have commented on the similarity in the histological appearance of the active testes of all three genera.

The only two accounts of the ultrastructure of monotreme spermiogenesis are in the report of Carrick (1977) which has been amplified by Hughes and Carrick (1978).

As might be predicted from the distinctive appearance of the spermatozoon, monotreme testes have some unusual features in comparison with those of other mammals. At the light microscope level, this is most readily apparent in the very long spermatid nuclei (which show varying degrees of helical coiling as they lie embedded deeply in the Sertoli cell cytoplasm) and also in the aggregation of large bundles of about twenty developing spermatids (Fig. 5).

The fine structure of spermiogenesis exhibits some features that are reminiscent of marsupials (see Harding *et al.*, 1976b). The most noticeable of these is the mode of formation of the early acrosome, the contents of which arise from sparse granular material in the pro-acrosomal *vacuole* rather than from a prominent pro-acrosomal *granule* as in eutherians. However, other features which are distinctly atypical of marsupial spermiogenesis include: the orientation of nuclear 'flattening' is in a lateral rather than a dorsoventral plane; and the definitive acrosome is a caplike structure investing the entire circumference of the anterior region of the nucleus, rather than being confined to the anterior portion of the dorsal nuclear surface.

The monotreme testis is distinguished from that of any other mammalian group by the enormous elongation of the developing spermatid nuclei as well as a most remarkable circumferentially arranged pattern of condensation in the chromatin of these nuclei (Figure 6). Although this pattern of condensation is uniquely different from that of any previously described mammal, it is quite similar to that seen in some avian species. However, Carrick (1977) in reviewing the extensive paper of Fawcett *et al.* (1971) pointed out that comparable patterns of chromatin condensation also occur in the testes of some invertebrates. It is therefore suggested that the characteristic pattern of chromatin condensation seen in *O. anatinus* might reveal more about morphogenetic function than it does directly about phylogeny (Carrick, 1977).

INTERSTITIAL TISSUE

The Leydig cells of the platypus testis have been studied in respect of the histological and histochemical changes related to the breeding season, as was discussed earlier in this paper (Temple-Smith, 1973). Griffiths and Elliott (pers. comm.) have observed similar histological changes in the interstitial tissue of echidnas.

At the ultrastructural level, Carrick (1977) has noted some distinctive features of the fine structure of the active Leydig cell of *Ornithorhynchus*. The Leydig tissue of the platypus contained abundant smooth endoplasmic reticulum (smooth

ER), mostly in the form of fenestrated cisternae or random tubules (Fig. 7). In some cases, the smooth ER was elaborated into whorls of concentric cisternae (Fig. 8).

The abundance of lipid droplets was another prominent feature of the cytoplasm of these cells. These were almost always found in a striking association with mitochondria, and a specialisation of the smooth ER was often associated with these organelles (Fig. 7).

The mitochondrial cristae were seen in some sections to be tubular in profile, and inclusions were sometimes present in the matrix. Nuclear pores were present in the envelope bounding the irregularly shaped nucleus, and in some sections channels were seen passing from these pores through the peripheral heterochromatin. Nucleoli may be present but were not particularly prominent.

The plasma membranes of the Leydig cells often had projections that interdigitated with other elements of the interstitial tissue. Free ribosomes were usually present within the cytoplasm of the Leydig cells and were typically most prominent in the perinuclear region. Lysosomes and related organelles were not common in the active testis of *O. anatinus*, and crystalloid inclusions have not been observed.

In summary, the appearance of the Leydig cells in the platypus testis was consistent with the description of such cells in other mammals, as outlined by Christensen and Gillim (1969). This is hardly surprising in view of the finding that large amounts of testosterone are secreted by the testes of this species (Carrick, 1977; Carrick & Cox, 1973, 1977). Further ultrastructural studies of these steroid secreting cells might lead to the discovery of distinctive morphological features which could be of significance in the cytochemical interpretation of androgen production.

EPIDIDYMIS

The epididymides of monotremes are very large in comparison to the equivalent organs in scrotal mammals. Although Temple-Smith (1973) considered the epididymides of the platypus to be "similar in structure to those of other mammals" and undoubtedly they share many common features of histology and function, it is also apparent from our preliminary results that there are some important ultrastructural differences.

The structure of the epididymis of *Tachyglossus* is the subject of a later paper (by Jones) in this symposium, and consequently no further consideration will be given to this aspect, except to note that MacKenzie and Owen (1919) considered that, although the epididymides of the platypus and echidna were basically similar, some structural variation did exist.

A few disparities are evident between our observations on the epididymis and those of Temple-Smith (1973). These differences may be attributable, in part,

to differences in technique. Our material has been fixed for electron microscopy (fixation by both perfusion and immersion, using both phosphate-buffered and cacodylate-buffered glutaraldehyde, followed by embedding in epoxy resin) whereas Temple-Smith (1973) used classical light microscope microtechniques (fixation in formal-saline followed by embedding in paraffin wax). Temple-Smith reported a very low concentration of spermatozoa in the efferent ducts and a progressive increase in sperm density throughout the epididymis, whereas our subjective estimates of sperm density indicate an initial dilution of sperm, then some degree of concentration. He also failed to observe the prominent peri-luminal vacuole array (Figs. 9 and 10) that has since been described in the mid-posterior part of the duct (Carrick, 1977). On histological criteria, Temple-Smith thought that the platypus epididymis could be divided into initial, middle and terminal segments, in a comparable manner to that reported by Glover and Nicander (1971) for a number of eutherian mammals. However, we incline to the opinion that this regionalisation is not so obviously apparent in the platypus, nor are the gross anatomical landmarks that readily lead to the division of the epididymis of scrotal mammals into caput, corpus and cauda regions at all obvious.

Both Temple-Smith (1973) and Carrick (1977) have suggested that the epididymis of the breeding platypus is a highly secretory organ. The former author described PAS positive secretory material in apical blebs of the glandular cells. The latter author observed cells throughout much of the epididymis that appeared to contain considerable amounts of presumptive secretory precursors in the bulging cell apices. Figure 10 illustrates the high level of apparent secretory and synthetic activity noted in the mid-posterior region of the epididymis. The peri-luminal clear vacuoles amongst the stereocilia appeared to result from apocrine secretory activity of some of the epididymal epithelial cells. However it should be noted that not all regions of the duct exhibit this array of vacuoles (Fig. 11).

Both these authors have commented on the large size of the epididymis and the possibility of a high degree of secretory activity in relation to the relatively small volume of other potential accessory seminal glands. Carrick (1977) has also suggested that the large size of the testes may also indicate a source of some part of the seminal plasma, but this seems a less likely source of such a secretion. Absorption and secretion are probably universal features of all mammalian epididymides, and we consider the platypus to be distinguished by an unusually high potential for epididymal secretory activity. It is perhaps significant that the major blood supply to the platypus epididymis appears to run to the expanded middle regions (Carrick unpublished observations), rather than to the anterior region as seen with the caput epididymidis of scrotal mammals.

The terminal parts of the epididymis have a very highly convoluted epithelial lining (Fig. 12). This is somewhat reminiscent of, though less extreme than, the convolution of the epithelium of the ductus epididymidis of the dugong, another testicond mammal (Marsh & Glover, 1978).

A dramatic sequence of maturational changes occurs in the sperm within the epididymis of a number of marsupials (Harding *et al.*, 1977). However, the most obvious changes in monotreme sperm are the loss of the cytoplasmic droplet (Hughes & Carrick, 1978) and the aggregation of bundles of several sperm.

This aggregation has been seen at both light microscope (Temple-Smith, 1973) and electron microscope level (Carrick unpublished observations). However, it is not clear at present whether the phenomenon is more like the 'rouleaux formation' seen in guinea pig sperm (Fawcett, 1975); or, as suggested by Temple-Smith (1973), the 'pairing' seen in the epididymis of American marsupials. (See Biggers, 1966).

Thus our present knowledge of the changes seen in monotreme sperm during epididymal transit seems to indicate more affinity with maturation in eutherian mammals than with the 'maturational' processes reported for marsupials.

ENDOCRINOLOGY

Changes seen during the annual cycle in the ultrastructure (unpublished observations) and histochemistry (Temple-Smith, 1973) of the Leydig tissue of the platypus testis, correspond with a pronounced variation of testosterone concentration in spermatic venous blood. A very substantial quantity of testosterone (about 400 ng/ml plasma) is measurable during the breeding season, but a considerable decline (to about 10 ng/ml plasma) is evident when the testis has involuted (Carrick & Cox, 1973, 1977; Carrick, 1977). Since testicular blood flow also decreases, this represents an even more drastic decline in steroid output. The secretion of the 400 ng/ml of testosterone into the spermatic vein results in a peripheral concentration of about 12 ng/ml plasma.

Chromatography on Sephadex LH-20 indicated that the major 17 β -hydroxy androgenic compound present in both the spermatic venous and the peripheral blood of the platypus was testosterone. However, it is likely that a minor, less polar compound (possibly dihydrotestosterone) was also present in the peripheral blood of the species (Figs. 14 and 15). The 17 β -hydroxysteroid profile for the spermatic venous plasma of the red kangaroo (*Megaleia rufa*) is also shown for comparison (Fig. 13). The much larger quantity of testosterone present in the platypus is obvious. It has also been reported (Carrick, 1977; Carrick & Cox, 1977) that readily detectable quantities of progestin-like materials were present in the peripheral blood of the male platypus but that oestradiol-17 β was not measurable.

The very high concentration of testosterone in spermatic venous plasma may be partially an effect of the high haematocrit commonly found in the species. However, the amount of testosterone secreted (24 ng/min/kg) is considerably larger than has been found in a number of marsupial species (up to about 11 ng/min/kg) (Carrick, 1977). Perhaps, it is relevant to consider these high levels of testosterone

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in relation to the large quantity of androgen-dependant tissue in the male platypus: testes, epididymides, Cowper's glands, crural glands and scent glands.

The concentration of testosterone in the spermatic venous plasma of a number of marsupial species has been found to be of the order of 100 ng/ml plasma (Carrick, 1977; Carrick & Cox, 1977). This is comparable with values found in eutherian species (ram, rat and stallion). Consequently, in this parameter of steroid function, the platypus appears to be at the high end of the mammalian range. However, the value of 12 ng/ml of peripheral plasma lies towards the middle of the considerable range of values of peripheral testosterone concentration that have been reported for eutherian mammals (from about 1 ng/ml to about 100 ng/ml). No data are available concerning the hormonal control of reproduction in the other two monotreme genera.

VASCULAR ANATOMY OF THE TESTIS

The blood supply to the testis of the two Australian monotreme genera has been recently discussed by Setchell (1970). He noted that, in the echidna, the spermatic artery ran from the aorta to the caudal pole of the testis by a fairly straight course. The artery was accompanied by a small vein, but the main venous drainage was via the cranial pole, thence to the renal vein. The artery was observed to enter the testis directly at the caudal pole without coursing over the testicular surface. The direct entry of the artery into the testis is common in testicond mammals, but unusual in scrotal mammals.

Setchell (1970) also described the vasculature of the platypus testis. The artery was again noted running to the caudal pole and directly entering the parenchyma. He cited the report of Manners-Smith (1894) that, although the artery and vein remain single, they follow a "somewhat tortuous" course. It was further noted that the entry of the spermatic artery at the caudal pole, rather than at the cranial pole where the efferent ducts exit, constituted an unusual arrangement.

Our own unpublished observations confirm the earlier reports for the platypus. Reference to Figs. 1 and 2 indicates the remarkable length of the artery and vein, considering the fairly short direct distance between the aorta and the testis. A complex coiling of the spermatic artery around a pampiniform plexus of veins, as seen in eutherian mammals with scrotal testes, does not occur; but convolutions of the artery are evident (Fig. 2).

It is also clear from Fig. 2 that the description by Setchell (1970) of the venous system of the platypus testis is incomplete: in addition to the main spermatic vein leaving the caudal pole of the testis, a secondary venous drainage emerges from the cranial pole. (This omission is understandable, since the material on which his description was based consisted of a pair of involuted testes which had a concomitant decrease in the prominence of the whole testicular vascu-

lature.) Thus, the pattern in *Tachyglossus* and *Ornithorhynchus* is similar, but with the degree of development of the caudal and cranial veins interchanged.

Very little is known of the testicular physiology of testicond mammals. However, the ubiquity of the scrotum in the Eutheria and Metatheria suggests that testicular migration out of the body cavity is of some fundamental significance. Several explanations have been offered for the phenomenon of testicular descent; the theories invoking an escape by the thermolabile testis from rising homoeothermic body temperatures have been most popularly accepted. Temple-Smith (1973) discussed the abdominal location of the platypus testis in relation to its deep body temperature (about 32-33°C: Grant, 1976) and concluded that the testicular temperature would be sufficiently low to preclude a selective pressure for the evolution of a scrotum. However, Carrick and Setchell (1977) have shown that the current theories on the evolution of testicular descent are inadequate in one or more respects, and that with particular reference to temperature, no correlation exists between position of the testes and body temperature.

Carrick and Setchell (1977) propose that vascular effects may be fundamentally involved in testicular descent, and for this reason the unusual vascular anatomy of the platypus testis is extremely interesting. Even though the testes of the platypus are in essentially the same position as those of Type 1 eutherian mammals (Carrick & Setchell, 1977) such as the elephant, the arteries are proportionately very much longer and more convoluted than the elephant's spermatic arteries, which are described by Setchell (1970).

The coiled spermatic artery of eutherian mammals (Type 6 testis position—Carrick & Setchell, 1977) results in a dramatic reduction in the *pulse pressure* of blood entering the testis, whilst causing relatively little drop in mean arterial pressure. The spermatic arterial rete mirabile of marsupials has been demonstrated to be functionally equivalent in this respect, although anatomically quite different. It will be most interesting to determine whether the spermatic artery of the platypus exhibits some intermediate degree of pulse attenuation as might be predicted from its elongated, though otherwise undifferentiated, morphology. No such measurements exist for any monotreme.

The close apposition of artery and vein may also make available a system of countercurrent exchange of some nutrient or metabolite of the platypus testis. Since only the major vein was cannulated during the acquisition of blood for steroid determination by Carrick (1977), the values obtained for testicular blood flow rate will almost certainly be an underestimate. (This will also apply to the testosterone secretion rate which should, therefore, be regarded as a minimal value). The total flow rates obtained ranged from about 0.9 ml/100 g testis per min in the non-breeding season, up to about 11.5 ml/100 g testis per min in the breeding season. The range of total blood flow values in eutherians reported by Setchell (1970) was quoted as 7.7 to 30 ml/100 g testis per min.

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COMPARATIVE PENILE MORPHOLOGY

It seems appropriate to end the detailed discussion of the reproductive tract of male monotremes with a description of the terminal part of that tract: the organ of intromission.

The penis of the adult platypus and echidna attains a length of about 7 cm. In the platypus, the shaft of the penis is armed with numerous recurved spines (Figs. 1 and 3). In both Australian monotreme genera, the glans penis is bifid, but this is more grossly obvious in the case of the platypus. In this species, the bulbous expansion of each branch of the glans bears an evertable group of, usually, four foliate papillae. Each papilla contains a branch of the divided seminal urethral duct. It is interesting to note that the left branch of the glans is visibly larger than the right and that this corresponds with only the left ovary being functional in the female platypus (Figs. 1 and 3).

In *Tachyglossus*, the bifid glans penis is again served by separate branches of the seminal urethra; however, the glans terminates in four flower-like rosettes of epidermal rays and a branch of the seminal urethra passes through the centre of each of the foliate papillae (Fig. 4). Thus, although they are superficially quite different in morphology, the penis of these two genera of monotremes are built on basically the same plan.

When the penis is not erect, it is located within a preputial sac adjacent to the cloaca (Owen, 1868; Griffiths, 1968; Temple-Smith, 1973). At present, there are no data to indicate the functional attributes of the unusual structure of the penis of either the platypus or the echidna.

CONCLUDING REMARKS

The monotremes are thought to have retained many of the physiological characteristics of the earliest mammalian forms, as well as some of the diagnostic anatomical characteristics of those ancestral types. However, as reported above and in a number of the other papers of this symposium, these characteristics often appear to be highly adaptive for the specialised life styles of the extant species.

The monotremes provide Australian researchers with a unique opportunity to contribute to an understanding of vertebrate phylogeny, and in few disciplines is this more relevant than for the development of mammalian reproductive processes.

Some aspects of the reproductive pattern of male monotremes render them especially valuable in discerning basic reproductive phenomena, since they have truly abdominal testes and distinct structural and functional changes during a relatively discrete breeding season.

It is apparent from the preceding discussions of this paper, that most of the really crucial features of the reproductive biology of male monotremes are still

relatively poorly known. The areas requiring the most urgent attention are outlined below:

The environmental and endocrine control (hypothalamus and pituitary) of the cycle of testicular activity needs to be determined. Temple-Smith (1973) was unable to achieve this with his field data, since the annual cycles of daylength, air temperature, water temperature and other environmental variables were too inter-related to allow discrimination between the various parameters. Controlled laboratory experiments will almost certainly be required to resolve this question.

The seasonal activity of the disseminate prostate and Cowper's glands and the composition and function of their secretions, need to be studied. Samples of monotreme semen should be obtained by electro-ejaculation and a detailed examination should be made of accessory gland ultrastructure.

The role of the scent glands and crural system in reproductive behaviour needs to be thoroughly evaluated. This will probably require a mixture of field and laboratory techniques.

The processes of spermatogenesis and 'maturation' in marsupials are substantially different in detail from the equivalent processes in eutherian mammals (Harding *et al.*, 1975, 1976 a & b). Our studies have, so far, revealed that the monotreme testis and spermatozoon have affinities with some aspects of each of the therian groups, as well as some highly distinctive features of their own (Carrick, 1977; Hughes & Carrick, 1978). Detailed studies of the ultrastructure of spermatogenesis and epididymal development of sperm need to be extended, using both transmission and scanning electron microscopy. For some aspects, this will need to be supplemented with histology and histochemistry.

There is no information on the frequency of the stages of the cycle of the seminiferous epithelium for any monotreme. More importantly, there is also a complete lack of data regarding the length of the cycle of the seminiferous epithelium or the duration of epididymal transit. It is of fundamental importance to determine whether the unusual spermatozoa require a radically different kinetic process and duration of spermatogenesis. This can only be resolved by appropriate quantitative histology and autoradiography techniques.

A detailed study of the epididymis of the monotremes should have a high priority. It is important to examine the structure of the duct epithelium at both the histological and ultrastructural levels, and to analyse the luminal contents (both structural changes in sperm and composition of the fluid). This would be particularly interesting in view of the suggestion that has been canvassed regarding a possible major contribution to the seminal plasma of the ejaculate, by the apparently high secretory epididymis.

The steroid endocrinological data that are available need to be extended in several ways (as discussed by Carrick, 1977). Perhaps, the most vital needs are for determinations of whether there is a pulsatile or diurnal secretory pattern of

REPRODUCTION IN MALE MONOTREMES

testosterone production, and a detailed study of the secretory pattern of testosterone throughout the annual breeding cycle. This could be correlated with ultrastructural changes in the Leydig cells and target tissues. It will also be very interesting to discern the secretory pattern and identity of a number of other steroids which have been observed in the peripheral blood.

The remaining urgent priorities are:

- (i) an accurate assessment of testicular blood flow rate (probably using a radio-isotope tracer 'wash-out' technique — Cr^{51} = EDTA);
- (ii) the measurement of any effect the rather long spermatic artery may have on haemodynamics (particularly any reduction in pressure pulse reaching the testis).

The incompleteness of the information on most critical features of the reproductive biology of male monotremes, precludes, for the present, meaningful speculation on the phylogenetic significance of these reproductive processes.

ACKNOWLEDGEMENTS

Dr Mervyn E. Griffiths kindly gave us the *Zaglossus* material, and Dr Peter Temple-Smith allowed us access to his thesis. Permits to work with these native mammals were provided by the National Parks and Wildlife Services and State Fisheries Services, of New South Wales and Queensland. Portions of this work were supported by the Australian Research Grants Committee and the Australian National Parks and Wildlife Service. We also wish to thank the numerous colleagues who have assisted in the field, and for other expert assistance and advice.

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LEGENDS FOR FIGURES

PLATE 1:

- Fig. 1:* Ventral view of the urinogenital system obtained from an adult male platypus in the breeding season. Note the relatively large size of the testes (*T*) and epididymides. The shape of the epididymides is also unusual, as is the blood supply (light coloured vessel which can be seen running to the expanded middle region of the right epididymis — the labelled one). The arrow heads indicate the origin of the long spermatic arteries at the aorta and their termination at the caudal pole of the testes. The absence of accessory seminal glands other than the single well developed pair of bulbourethral or Cowper's glands (*G_b*) and inconspicuous disseminate prostatic urethral glands (*Uap*)— is noteworthy. *B* bladder; *C* cloaca; *K* kidney; *P* penis; *U* ureter. x 0.65.
- Fig. 2:* A magnified view of the left testis (*T*) seen in Fig. 1 illustrates the convoluted course of the spermatic artery (*As*). A satellite vein (*Vsp*) accompanies the artery to the posterior or caudal pole of the testis, with an auxiliary drainage (*Vsa*) from the anterior or cranial pole. Testicular veins (*Vt*) can be observed emerging from the parenchyma to run on the testicular tunic to the poles. x 1.85.
- Fig. 3:* A magnified view of the penis seen in Fig. 1. The left (*L*) and right (*R*) glans are indicated and the four everted foliate papillae (*P_f*) on each glans are clearly shown. Numerous keratinous spines (*Sk*) cover the surface of the penis. x 3.
- Fig. 4:* The penis of adult echidna is illustrated. The two rosettes (*Ro*) comprising the right half of the bifid glans are arrowed. x 2.25.

PLATE 2:

- Fig. 5:* Light micrograph of the active testis of a platypus. The abnormally long corkscrew shaped nucleus of late stage spermatids is distinctive. These can be seen in longitudinal section (*Nsl*) and in transverse section (*Nst*). The formation of aggregations of developing spermatids at various steps in spermiogenesis is evident. *BV* blood vessel; *C_L* Leydig cell. x 850.
- Fig. 6:* Longitudinal section through condensing spermatid nucleus (*N*). The longitudinal distribution of the foci of chromatin condensation (arrowed), suggest a loose helical pattern. The transverse sections (*M_c*) of the microtubules of the manchette demonstrate its circumferential arrangement at this state of development. *C_s* Sertoli cell cytoplasm; *C_t* spermatid cytoplasm. x 29,800.

PLATE 3:

- Fig. 7:* Leydig cell of *O. anatinus* showing prominent lipid droplets (*L*). Smooth endoplasmic reticulum (*ER_s*) is also abundant. Note the intimate association of lipid droplets with mitochondria (*MT*). Arrows indicate channels through heterochromatin adjacent to nuclear pores. *I_m* mitochondrial inclusion; *N* nucleus; *R* ribosomes. x 48,300.
- Fig. 8:* Leydig cell showing concentric whorls of smooth endoplasmic reticulum (*ER_{sw}*). *L* lipid droplet; *MT* mitochondrion; *N* nucleus. x 29,800.

PLATE 4:

- Fig. 9:* Light micrograph of the 'body' region of the epididymis of a platypus in breeding condition. Numerous sperm can be observed in the epididymal lumen (*Le*), around which is a remarkable array of vacuole-like structures (*Ev*). Intertwined sperm occur occasionally in small groups (arrow). *Ee* epithelium of ductus epididymidis. x 530.
- Fig. 10:* Low power electron micrograph of the same region of the epididymis as illustrated in Figure 9. The bulging apical portion of an epithelial cell appears to have ruptured (arrowed). The discharged contents (also seen in other cells — double arrow) appear to be dispersing to form the large vacuole-like structures (*Ev*) associated with the long stereocilia (*SC*). Numerous sperm are present in the lumen. x 2,900.
- Fig. 11:* Electron micrograph of the 'head-body' region of the epididymis illustrated in Figures 9 and 10. Long stereocilia (*SC*) are present but the vacuole-like structures seen in more posterior regions of the duct are not encountered. Several transverse sections of sperm are seen in the lumen. x 16,800.
- Fig. 12:* Light micrograph of the terminal region of the epididymis. Note the convoluted appearance and the connective tissue septa. Spermatozoa (*Sz*) can be seen in the lumen of the duct (*Le*). x 530.

PLATE 5:

- Fig. 13:* It can be seen that by far the major component androgen in the spermatogenic plasma of *Me. rufa* was testosterone. A second minor component, of rather greater polarity, appears to be present.
- Fig. 14:* Testosterone again predominated as the significant 17β -hydroxysteroid, in the spermatogenic plasma of the platypus in the breeding season. (In fact, in this instance, it was virtually the only reactive material present.)
- Fig. 15:* Peripheral plasma was obtained from the same animal which provided the spermatogenic venous sample data of Fig. 14. It again appeared that testosterone was the major component, but it is likely that a second less polar substance was present. The relative concentrations of testosterone present in spermatogenic venous and peripheral plasma should be noted.

In these profiles, the dark curve represents steroid assayed as testosterone equivalents; the white curve represents the ^3H -testosterone tracer (recovery label).

PLATE 1:

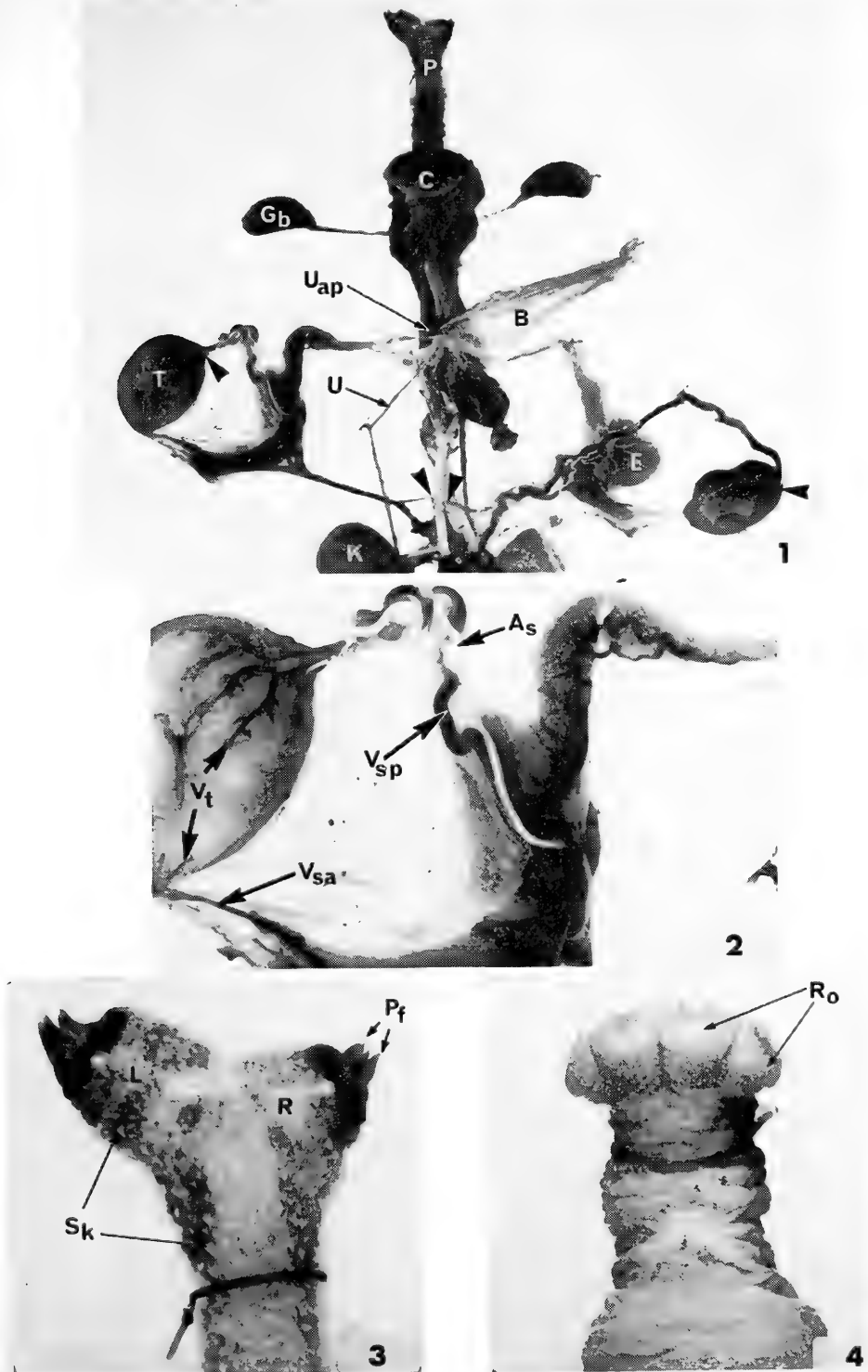


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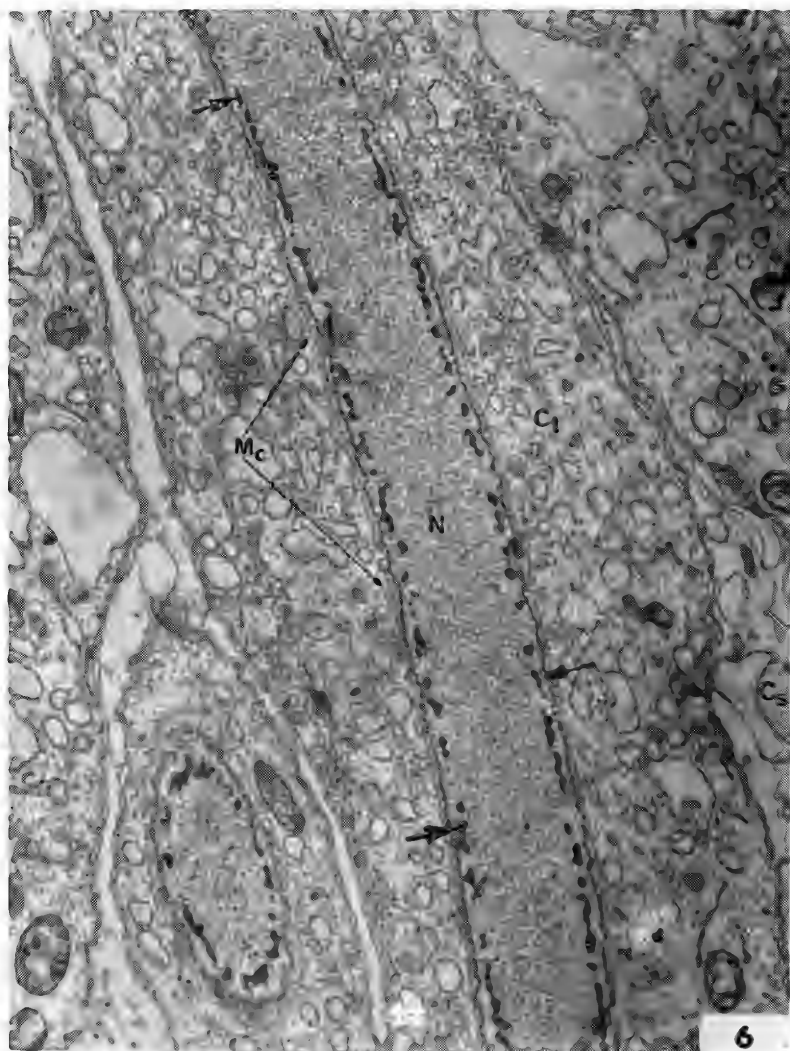
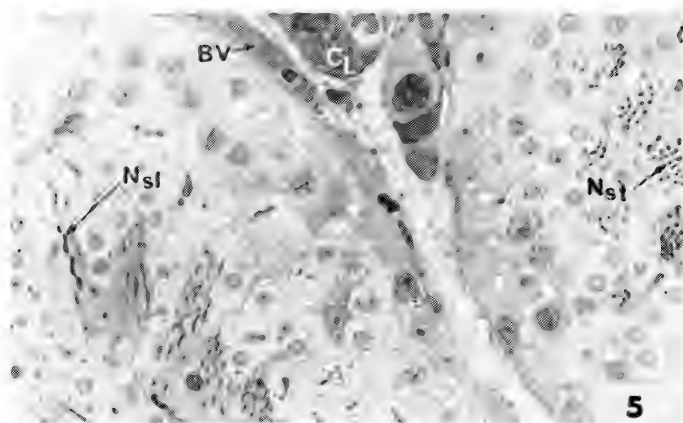
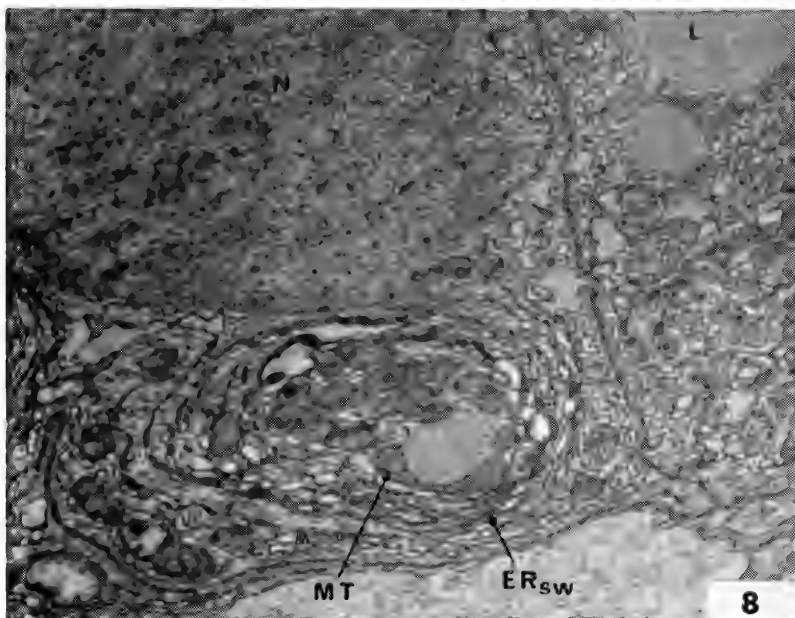
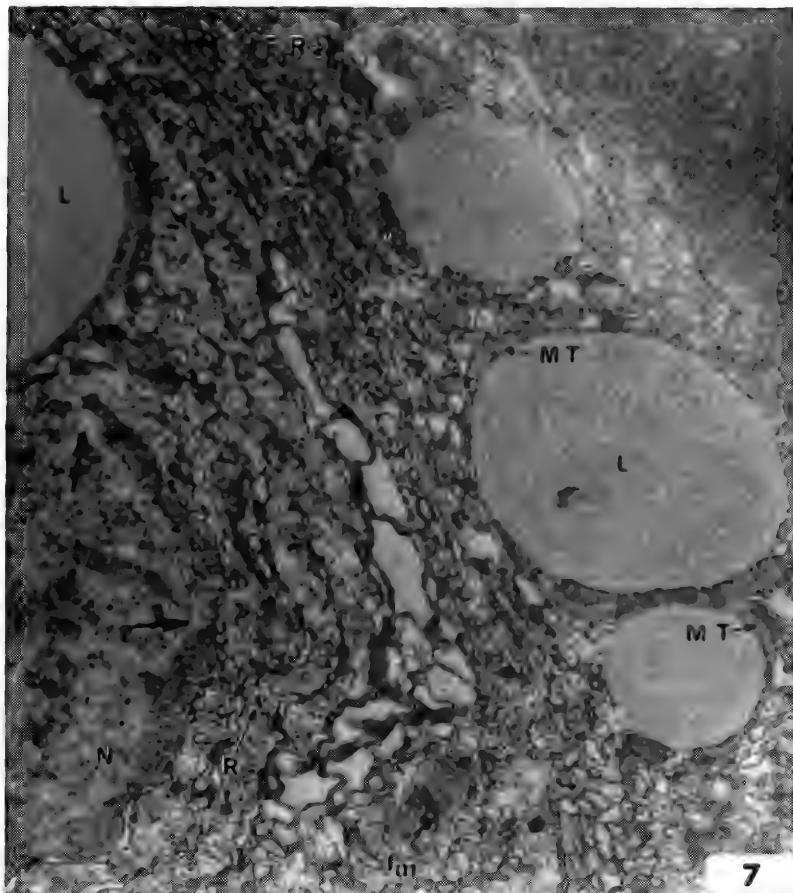
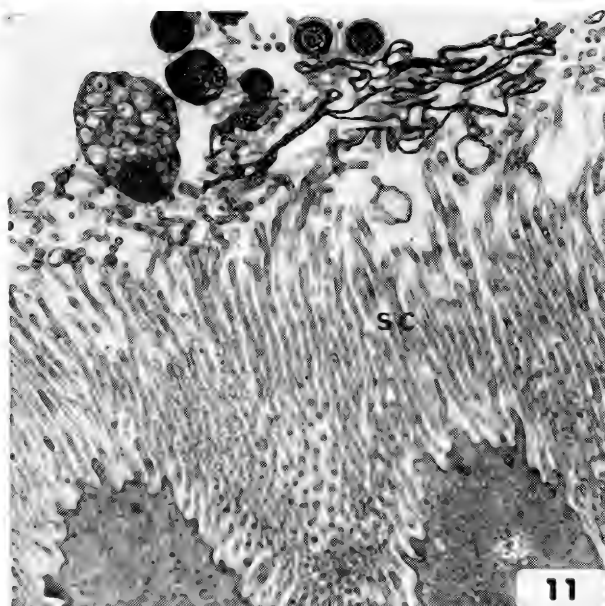
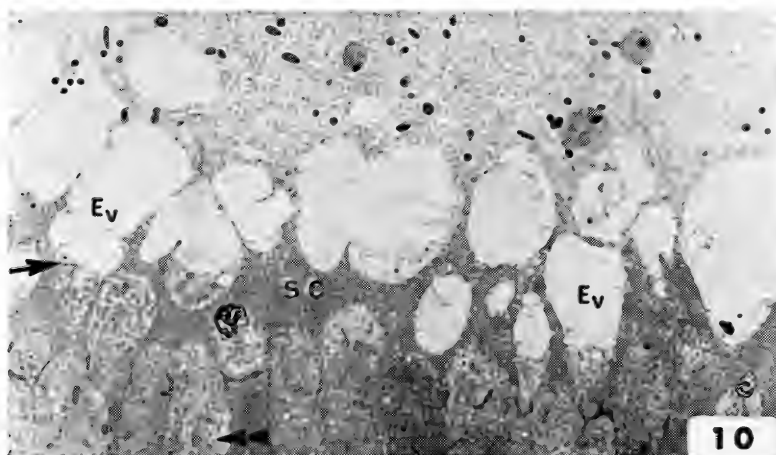
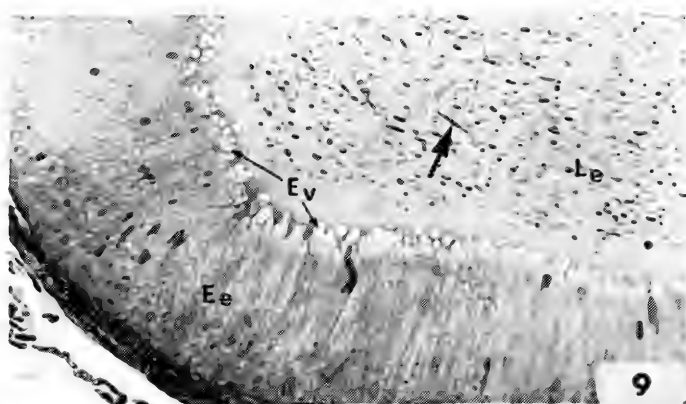


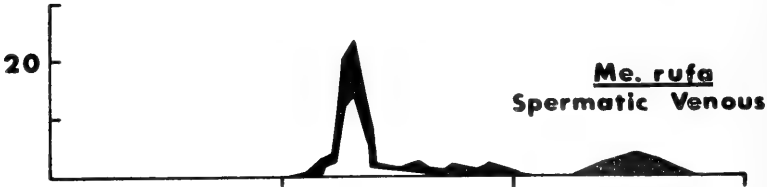
PLATE 3:



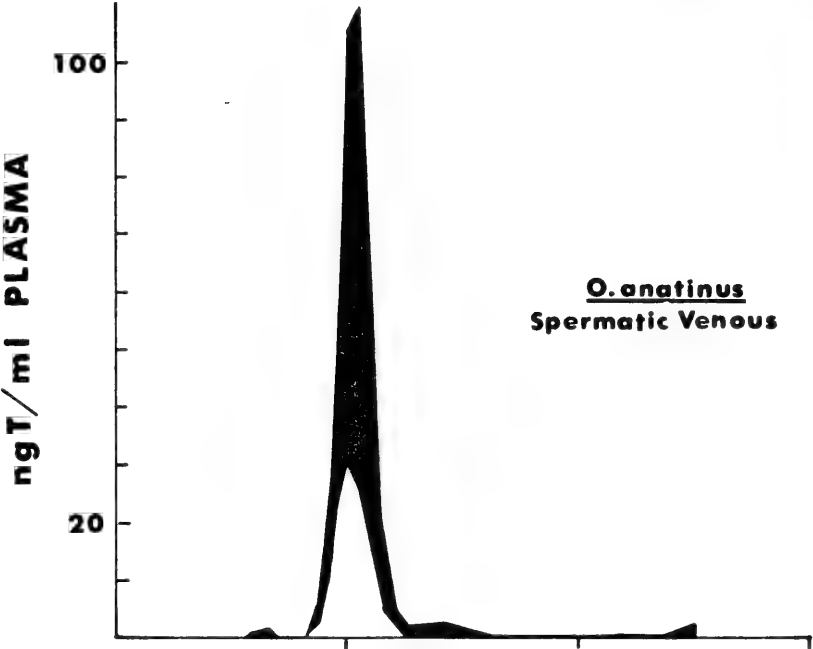


LH20/CPBA PROFILE FOR 17 β OH STEROID
IN PLASMA

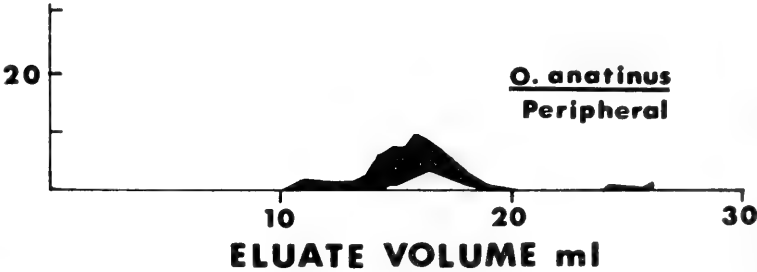
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14



15



Reproduction in Female Monotremes

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As early as 1834, Sir Richard Owen suggested that reproduction in female monotremes and marsupials might profitably be compared with that seen in certain sauropsid vertebrates. Owen regarded both the marsupials and the monotremes as an aberrant group of mammals characterised by an ovo-viviparous mode of reproduction. However, half a century elapsed before Caldwell and Haake independently reported in 1884 that monotremes laid cleidoic eggs and that the vitellus exhibited meroblastic cleavage comparable to that of sauropsid vertebrates (Caldwell 1887). The fullterm egg of the platypus was found by Caldwell (1887) to contain an embryo with a degree of development equivalent to that of a chick of about 36 hr of incubation. Wilson and Hill (1908) also reported that two sub-terminal intra-uterine platypus eggs contained embryos with seventeen or eighteen pairs of somites. Similar findings were reported by Hughes (1974a) and Hughes *et al.* (1975) who made observations on two of a total of three fully developed intra-uterine platypus eggs that were recovered from an animal one week following capture on 28th Sept., 1973, near Yass, New South Wales. The eggs were oval and of approximately equal size. The major and minor axes of the parchment-like shell were 17mm and 15mm respectively. When the shell of one of the eggs was removed it was found to contain a "pre-fetal" embryo with an overall length of 15mm and possessing about 20 pairs of somites. The anterior portion of the neural tube exhibited well differentiated optic vesicles and rudiments of a head fold had developed. Although no embryonic blood vessels were seen, blood islands had commenced to form. Hughes (1974a) found that the stage of embryonic development that was attained when the monotreme egg is laid was comparable to that of marsupials at about the time of the rupture of the shell membrane that completely invests the developing intra-uterine embryos. Carrick (1977) recovered two newly laid eggs from a captive platypus. The dimensions of one of these eggs are shown in Figure 1. The female platypus was captured on the night of 8th September, 1976 and the eggs were laid some time between 0900 and 1500 on the 17th September, 1976. The early literature on the reproduction and the embryology of the monotremes is reviewed by Griffiths (1968).

The formation of the corpus luteum from the post-ovulatory ovarian follicle of monotremes was described by Caldwell (1887). However it was Hill and

Gatenby (1926) who made the important observation that this structure was apparently a functional endocrine gland that regulated uterine proliferation during the period when the developing cleidoic egg of monotremes was retained within the uterus. The fragmentary data on the length of gestation period of monotremes includes the observation by Broom (1895) who reported that the interval between mating and egg laying in the echidna was about 28 days. The observations by Carrick (1977) indicated that this period in the platypus might be expected to be greater than 10 days.

The present paper provides confirmatory evidence for the endocrine function of the corpus luteum of the platypus and considers reproduction in monotremes as it relates to the possible course of the evolution of viviparity within the mammalian group of amniote vertebrates. Light microscope and electron microscope observations on the ovary, the egg, and the reproductive tract will be considered in relation to the assay of peripheral blood plasma for gonadal steroids. The significance of these observations will be discussed in relation to the early literature. The authors have made no personal observations on lactation in monotremes and for further details on this subject the reader should consult Griffiths (1965, 1968) and Griffiths *et al.* (1969). In the text platypus indicates *Ornithorhynchus anatinus*, and echidna indicates *Tachyglossus aculeatus*. Almost nothing is known of reproductive processes in *Zaglossus*.

THE FEMALE REPRODUCTIVE SYSTEM

The reproductive system of a female platypus was obtained during the preovulatory phase of the breeding season is shown in Figure 2. Although the right ovary is universally rudimentary in the platypus, both the right Fallopian tube and the right uterus are only marginally less developed than those on the left functional side. Carrick (1977) found that the right rudimentary ovary exhibited neither compensatory hypertrophy nor the formation of an ovotestis at 10 weeks after removal of the left functional ovary despite the fact that this sexually mature platypus was examined at the height of the breeding season. Flynn (1930) reported that both ovaries were functional in the echidna.

With the onset of the breeding season the surface of the left functional ovary of the platypus progressively exhibits an unevenness of the surface contour as the yellow pigmented ovarian follicles protrude up to and beyond 2-4mm from the ovarian surface. The ovaries strikingly come to resemble those of sauropsid vertebrates at the height of the breeding season and it was this that led the early investigators to suspect that monotremes might be oviparous.

The basic arrangement of the reproductive ducts of the female platypus, illustrated in Figure 2, is similar to that reported for the echidna (Griffiths 1968).

The ovaries of both monotreme species are invested by exceptionally well developed infundibular funnels that convey the ovulated eggs into relatively long but poorly convoluted Fallopian tubes. The paired uteri enter separately into a

REPRODUCTION IN FEMALE MONOTREMES

long unpaired median urogenital sinus, there being no vagina in monotremes. The ureters of adult female monotremes enter separately into the urogenital sinus near the neck of the bladder (Griffiths 1968). This is the condition exhibited during embryonic development in both the marsupials and the eutherian mammals, however as organogenesis proceeds the ureters of the non-monotreme mammals are progressively incorporated into the neck of the urinary bladder. The urogenital sinus of monotremes enters into a cloaca so that eggs, urine and faeces pass to the exterior via the same cloacal sphincter. Owen (1968) described the monotreme clitoris as a 'little flattened body shaped like a heart on playing cards'. Two small round flattened glands, the homologue of Cowper's glands, were located at the base of the clitoris.

OOGENESIS

The surface of the platypus ovary exhibits only small follicles of less than 2.0mm in diameter for much of the year. However during the immediate pre-ovulatory period ovarian follicles have a diameter of between 4.0mm to 4.5mm.

The developing ovarian follicles of monotremes resemble those of sauropsid vertebrates in that no antral cavity forms between the follicle cells that invest the developing primary oocytes (Figures 3 and 4). Consequently the ovarian follicles of monotremes differ from those of marsupials and eutherian mammals by lacking a structure during oogenesis which is the homologue of the Graafian follicle. However Caldwell (1887) reported that a small quantity of fluid (pro-albumen) was secreted by the follicle cells so as to separate them from the zona pellucida of the pre-ovulatory oocytes of the echidna. Flynn and Hill (1939) considered Caldwell's finding of singular importance since in their opinion this secretion was the homologue of the liquor folliculi of the Graafian follicle of other mammals. However further research will be needed in order to sustain this interpretation and it should not be taken as confirmed that a rudimentary pre-ovulatory Graafian follicle occurs in monotremes.

The developing primary oocytes contained within the ovarian follicles consist of a yolky and a cytoplasmic component of the vitellus which is invested by two egg membranes: The vitelline membrane and the zona pellucida. As yet no ultra-structural accounts are available of the development of either of these two egg membranes or of the vitellus.

VITELLUS AND VITELLINE MEMBRANE

The vitellus of pre-ovulatory oocytes of monotremes has been reported to have a diameter of about 3mm to 4mm (Caldwell 1887, Flynn 1930, Flynn and Hill 1939), and in comparison to that of marsupials and eutherian mammals this diameter is respectively about 15 and 25 times greater.

The vitellus of the pre-ovulatory egg of monotremes consists of a thin peripheral rim of cytoplasm with the nucleus located within a small lenticular blastodisc

of cytoplasm that subsequently undergoes a sauropsid-like meroblastic cleavage following fertilisation. The peripheral rim of cytoplasm invests a medullary region of yolk spheres (Figure 4) that comprises almost the entire volume of the vitellus and as in sauropsid vertebrates constitutes an important ovarian source of embryonic nutrients. The yolk spheres of the medulla of the vitellus are synthesised during a terminal vitellogenic phase of oogenesis. Neither marsupials nor eutherian mammals exhibit a comparable phase of vitellogenesis during oogenesis, so that the so-called yolk bodies of the eggs of these mammals are in fact relatively rarely encountered cytoplasmic inclusions that frequently exhibit a complex membranous structure not yet demonstrated to be comparable to the yolk spheres of the monotreme egg in either origin and ultrastructure, or in chemical composition. The vitellus of many marsupials is characterised by a vacuolated medullary region (Hughes unpublished), however, as yet the relationship of the contents of these vacuoles to the yolk-spheres of monotremes remains to be established. A phenomenon known as yolk elimination has been reported to occur during early cleavage in certain marsupial species. However an ultrastructural study of this process in the marsupials *Isoodon macrourus* and *Potorous tridactylus* (Hughes unpublished) has shown this to be the elimination of accessory cytoplasm and not definitive yolky material. It is considered probable that a similar finding might be anticipated when ultrastructural studies of the early cleavage stages have been made or a wider variety of other marsupial species. In this context it is unfortunate that ultrastructural observations of the elimination of accessory cytoplasm during the early cleavage stages in the marsupials *Perameles nasuta* and *Isoodon macrourus* were interpreted by Lyne and Hollis (1976) as yolk elimination.

The vitelline membrane is the cell membrane of the egg, and its numerous outwardly projecting microvilli confer a striated appearance immediately beneath the zona pellucida of follicles containing oocytes in the immediate pre-vitellogenic phase (Figure 3). The extreme abundance of the microvilli of the vitelline membrane of rapidly enlarging primary oocytes is evidence of its high absorptive capacity.

ZONA PELLUCIDA

The zona pellucida is a matrix deposited, during the ovarian development of the primary oocyte, between the interdigitating microvilli of the vitelline membrane and those arising from the investing ovarian follicle cells. The zona pellucida is permeable to nutrients and wastes (Hughes and Shorey 1973) and serves to isolate the developing egg from maternal tissues. An ultrastructural investigation has not yet been made of either the development or the fate of the zona pellucida for monotremes, nor has it been confirmed that the monotreme zona pellucida exhibits the histochemical properties of a weakly acidic glycoprotein as has been reported for marsupials and eutherian species (Hughes 1947b, 1977). The zona pellucida of the platypus has a maximum thickness of about 11 μm at about the onset of vitellogenesis, however it thins to less than 0.5 μm in the pre-ovulatory

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oocyte (Hughes 1977). This variation in the thickness of the zona pellucida of the platypus is illustrated in Figures 3 and 4. These observations confirm the early reports of Caldwell (1887) and Flynn and Hill (1939) that the maximum thickness of the monotreme zona pellucida occurred near the time when vitellogenesis began in primary oocytes. However, Caldwell (1887) mistakenly named the zona pellucida, the vitelline membrane.

Flynn and Hill (1947) found that a very thin zona pellucida was closely adherent to the basal surface of a compacted zona—albumen layer that ranged in thickness from 9 μm to 18 μm in early intra-uterine echidna eggs of from 4.0mm to 6.0mm in diameter. These eggs contained embryos that varied in stages of development from the formation of the primitive endoderm to the presence of the early primordia of the primitive streak. It is uncertain how the zona layer of of from 3.6 μm to 28 μm in thickness reported from echidna and platypus eggs by J. P. Hill (1933) relates to the findings of Flynn and Hill (1947).

BREEDING SEASON

The echidna breeds in eastern and south-eastern Australia from about the end of June until early September (Griffiths 1968). During this time a single egg was usually ovulated although up to three eggs may be present (Flynn 1930). In the platypus, the earliest and the latest dates that Burrell (1927) recovered eggs from nesting burrows were the 24th August and 22nd October respectively. The maximum number of eggs ovulated was three, however two eggs were most frequently recovered from the nesting burrows.

The immediately pre-ovulatory period of monotremes was characterised by the emission of the first polar body from the germinal disc of the volky vitellus and, as in the majority of mammalian species, the chromosomes of the nucleus of the secondary oocyte were arranged as a metaphase plate in preparation for the emission of the second polar body (Flynn and Hill 1939). The ovum of between 3 to 4 mm in diameter is ovulated into the infundibulum of the Fallopian tube.

MUCOID COAT AND EGG SHELL

The mucoid coat and the egg shell of monotremes are tertiary egg membranes, typical of the cleidoic eggs of sauropsid vertebrates, and are both contributed to the ovulated eggs during their passage through the Fallopian tube or in the uterus.

The mucoid coat is the first to be deposited and is a sulphated acidic glycoprotein which is derived from membrane bound precursors within the cytoplasm of non-ciliated cells (Figure 5) that are distributed throughout the entire luminal epithelium of the Fallopian tube of the platypus (Hughes 1974b). An account of the origin of the precursors of the mucoid coat in monotremes was given by C. J. Hill (1933, 1941). She considered that two separate layers of mucoid coat

were present and that each layer was contributed by a separate cell type located at different levels within the Fallopian tube. However both unpublished ultrastructural observations and histochemical studies (Hughes 1974b) suggest that the mucoid coat precursors of the platypus are a homogeneous single entity and consequently the presence of the two layers could represent an artefact of fixation.

Virtually identical histochemical properties have been reported by Hughes (1974b) for the precursors of the mucoid coat in the platypus and in a wide variety of marsupial species as well as for the rabbit. A strongly acidic glycoprotein tertiary investment was considered by Hughes (1977) to be characteristic of the eggs of a wide variety of vertebrate species so that the mucoid coat of monotremes and marsupials should be interpreted as the product of a long evolutionary history. In a review of the literature for eutherian mammals and marsupials Hughes (1974b) found that the mucoid coat precursors or their homologue was stimulated by oestradiol-17 β , however this remains to be demonstrated for monotreme species.

Flynn (1930) reported that the fully formed mucoid coat of an unsegmented early intra-uterine egg of the echidna varied in thickness from 17 to 30 μm and this falls within the lower range of thickness (15 to 150 μm) reported for the mucoid coat of marsupial species Hughes (1974a, 1977). Flynn and Hill (1947) found that the mucoid coat (albumen layer) persisted in the echidna as a compacted zona pellucida-albumen layer until at least the establishment of the early primordia of the primitive streak. The thickness of this combined membrane was 9 to 10 μm in a 4.0mm echidna egg that contained an embryo with the primitive endoderm established.

A strongly sulphated glycoprotein coat has been reported by Hughes (1977) to occur on the inner surface of the shell of a full-term platypus egg. The thickness of this membrane was approximately 2 μm and its ultrastructure resembled that of the mucoid coat reported for the marsupial egg (Hughes 1974b). Likewise ultrastructural observations revealed that a similar membrane was associated with the inner surface of a fully formed echidna egg. On this basis Hughes (1977) has tentatively concluded that these membranes represented the persistent mucoid coat of the monotreme egg. However according to Caldwell (1887) the albumen layer (mucoid coat) entirely disappears by the time that the intra-uterine monotreme egg had expanded to a diameter of 6.5mm. Caldwell (1887) also reported that the zona pellucida thickened within the female reproductive tract and came to lie close to the egg shell. Further studies are therefore necessary in order to determine whether the zona pellucida becomes modified by swelling or by the additions of secreted tertiary material from the reproductive tract and also to establish the nature of any relationship between the zona pellucida, mucoid coat and the strongly sulphated membrane that lines the inner surface of the fully formed monotreme egg shell.

In marsupials the mucoid coat was found to be readily permeable to nutrients and wastes (Hughes and Shorey 1973). It rarely persisted beyond the bilaminar

blastocyst stage (Hughes 1974a). Comparable data is not yet available for monotreme species.

In monotremes the egg shell of structural protein is the second type of tertiary egg membrane contributed to the cleidoic egg during its period of retention within the female reproductive tract.

In the newly-laid monotreme egg, the shell consists of three major structural components and an outer more dispersed cuticular fourth investment (J. P. Hill 1933). The structure of the egg shell of monotremes is illustrated in Figures 6, 7, 8, 9.

The first of the three major structural components of the monotreme egg shell was described by J. P. Hill (1933) as a thin compacted layer ranging in thickness, according to stage of development, from 1.3 μm to 3.6 μm . When fully formed the basal layer may exhibit a slightly laminated ultrastructure (Figure 8). C. J. Hill (1933, 1941) believed that this layer was contributed to the egg by the secretions of tubal glands that penetrated the luminal epithelium of the lower third of the Fallopian tube. Hughes (1974b, 1977) reported that disulphide groups characteristic of the ovokeratinous shell membranes of many vertebrates were histochemically detected in the presumptive shell membrane precursors within these distinctive tubal glands of the platypus, and that similar histochemical properties were also characteristic of a component of the secretory products within the uterine endometrial glands of the platypus.

The size of the tubal glands that penetrated the lower third of the Fallopian tube of a platypus in an immediately pre-ovulatory condition (4mm-4.5mm ovarian follicles) were reported by Hughes and Shorey (1972) and Hughes (1974b) to be much larger than the uterine glands and were lined exclusively by non-ciliated columnar secretory cells. The post-ovulatory tubal glands are also highly active (Figure 10). The tubular glands of the uterine endometrium were, by contrast, lined by a mixed epithelium that consisted of both ciliated and non-ciliated cells (Figure 11).

According to J. P. Hill (1933) the shell of the marsupial egg does not advance beyond the stage of the basal layer of the monotreme shell. However this should not be interpreted to indicate that both are homologous structures. This was pointed out by Hughes (1974b) who found that in the marsupial *Trichosurus vulpecula* the Fallopian tube lacked tubal glands and that in this marsupial the entire shell membrane arose from the secretions of the uterine glands.

The basal layer of the monotreme egg shell becomes invested by irregularly shaped rodlets of apparently similar material to that initially deposited in the Fallopian tube. These rodlets were considered by C. J. Hill (1933, 1941) to have arisen from both the tubal glands as well as from the uterine endometrial glands. However her account of this aspect lacks conviction, so that the origin of the rodlet layer of the monotreme egg requires further investigation. The latter period of the

deposition of the rodlet layer is accompanied by the growth of the egg (J. P. Hill 1933) that results from the passage through the egg shell of nutrients that arise from the secretions of the greatly proliferated uterine endometrium. In the latter connection the ultrastructural observations of Hughes and Shorey (1972) are of particular interest in that the uterine endometrium of an immediately pre-ovulatory platypus (4mm-4.5mm ovarian follicle) resembled the luteal phase of marsupial species (Figure 11). This unexpected secretory activity of the uterus was thought to be related to both the formation of the complex tertiary egg coats as well as to the extensive intra-uterine growth of the egg. By the time the egg has attained a diameter of about 10mm the rodlets have attained their maximum length ranging from about 10 μm to 20 μm (J. P. Hill 1933). The growth of the intra-uterine egg results in stretching of the basal layer of the egg shell and the separation of the rodlets so that the space between them becomes impregnated by a clear matrix.

A coarsely granular secretion of the uterine endometrial glands of monotremes was considered by C. J. Hill (1933, 1941) to be the precursor of the massive protective matrix layer of the shell. The deposition of this third component of the shell onto the surface of the rodlet layer was completed only when the egg had reached its full size with axial measurements of approximately 15mm x 17mm. J. P. Hill (1933) reported that the fully developed matrix layer of monotremes egg shells ranged in thickness from 130 μm to 208 μm . The deposition of the shell with a concurrent spectacular growth of the intra-uterine cleidoic egg (Figure 6) is a feature of monotreme reproduction not found in the oviparous sauropsid vertebrates and it was J. P. Hill (1933) who noted that the unique structure of the monotreme egg shell was functionally adapted to permit this growth to occur.

The egg shell that invested the fully developed intra-uterine platypus embryo collected by the present authors (Figure 7) consisted of three concentrically arranged components. The compact inner basal layer had a thickness of 2 μm and exhibited a fine granular ultrastructure. The basal layer was in turn invested by a relatively open meshwork of rodlets with a height of approximately 20 μm . An outer matrix layer with a thickness of 49 μm consisted of loosely arranged but relatively large irregular shaped particles. It should be noted that this layer was much thinner than the 130 μm to 208 μm previously reported by J. P. Hill (1933) for full-term monotreme eggs. The total thickness of the full-term egg shell collected by the present authors were equivalent to the overall thickness of the double shell membrane of the domestic fowl, however, important chemical and structural differences exist (Hughes 1977).

In the platypus the egg shell exhibited a weak reaction for disulphide groups using histochemical staining for sulphonic acid groups, following the oxidation of the sectioned egg shell with performic acid. The platypus egg shell was not detectably degraded after four days of incubation in a solution of the proteolytic enzyme pronase (2mg pronase/ml Tris buffer pH 8 at 37°C).

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Scanning electronmicroscopy of the surface of the full-term intra-uterine platypus egg (Figure 9) showed a loose arrangement of irregularly shaped particles that contrasted with the fibrous structure of the shell membrane of the domestic fowl (Hughes 1977).

The mean equivalent pore diameter of the shell membrane of the domestic fowl has been reported to be about $1\text{ }\mu\text{m}$ (Wolken 1951). However in the platypus, erythrocytes (with a diameter of $5.5\text{ }\mu\text{m}$ after fixation) liberated from the endometrial blood vessels during the recovery of the egg had penetrated both the outer matrix layer as well as the rodlet layer in large numbers, however none were found within the compact basal layer.

Hughes (1977) reported that the fully developed egg shell of the echidna had an essentially similar structure (Figure 8) to that of the full-term platypus egg (Figure 7), thus confirming the earlier observations by J. P. Hill (1933). The monotreme egg shell is obviously permeable to nutrients as its diameter increases from about 3-4mm at the beginning of the period of intra-uterine retention (gestation) to about 15mm x 17mm at the close of gestation when the enclosed pre-fetal embryo has attained an overall length of about 15mm and possesses about 20 pairs of somites. In the marsupial *Trichosurus vulpecula* the dense granular lattice of the thin shell membrane was reported by Hughes and Shorey (1973) to be permeable so as to permit the free passage of nutrients and wastes. The dense granular matrix of the platypus egg shell exhibits a similar ultrastructure to the shell membrane of *Trichosurus vulpecula* (Hughes 1977). It is also of particular interest that the ultrastructure of the shell membrane precursors within the secretory cell cytoplasm of the uterine glands of the platypus (Figure 11) strikingly resembled those reported by Hoffer (1971) within the glands of the isthmus region of the avian oviduct, thus suggesting a basis for a possible homology between these two structures.

As in monotremes and marsupials, the shell membrane of the avian egg is also permeable (Simkiss 1967, see also Hughes 1974b). The presence of a permeable shell membrane in the cleidoic eggs of vertebrates was regarded by Hughes (1977) to be of special significance in the evolution of mammalian viviparity. This was considered to have enabled the yolky vitellus of the cleidoic egg to have become displaced by nutrients of uterine origin as the major source of embryonic nutrition and consequently to have facilitated the progressive reduction in the size of the vitellus. The extremely small size of the mammalian vitellus became possible with the evolution of a functional corpus luteum and the consequent insertion of a uterine luteal phase into the reproductive cycle. In this context the reduced size of the vitellus of the cleidoic eggs of monotremes and the recent confirmatory evidence by Hughes *et al.* (1975) and Carrick *et al.* (1975) for a true luteal phase in monotremes is of special significance.

CORPUS LUTEUM

The most significant contribution to our current understanding of the evolutionary significance of reproduction in female monotremes was, without doubt,

presented by Hill and Gatenby (1926). Their histological evidence convincingly showed that after ovulation the sauropsid-like ovarian follicle of monotremes formed a structure which they correctly interpreted as equivalent to the functional corpus luteum of other mammals. They believed that the corpus luteum acted as an endocrine gland which produced a uterine growth-stimulating hormone that regulated the secretory and nutritive activity of the uterine endometrium during pregnancy.

The ultrastructure of one of three corpora lutea of 4.5mm in diameter obtained by the authors from a platypus at full-term pregnancy was reported on by Hughes *et al.* (1975) and is shown in Figure 12. The luteal cells contained abundant smooth endoplasmic reticulum (ER_s) and mitochondria (MT). The luteal cell surface exhibited complex folding and interdigitated with adjacent cells. Numerous membrane bound granules (G₁), with a diameter of about 400nm were present within the cytoplasm. Carrick (1977) suggested that these granules may be comparable to those reported in the corpus luteum of the sheep by Gemmell *et al.* (1974), which were believed to be involved in the secretion of progesterone. Hughes *et al.* (1975) noted that the luteal cells of the platypus corpus luteum had a comparable ultrastructure to that of viviparous mammals as well as the lack of luteal necrosis at full-term in the platypus.

STEROID HORMONES IN PERIPHERAL BLOOD PLASMA

Carrick *et al.* (1975) and Carrick (1977) have compared the concentrations of progesterone and oestradiol—17 β in the peripheral blood plasma of the full-term pregnant platypus with those found in two non-pregnant adult females, an ovariectomised female and male platypus. These data are shown in Table 1 and indicate that the highest concentrations of both these hormones occurred in the pregnant animals. Thus the hormonal steroids known to be associated with the maintenance of pregnancy in metatherian and eutherian mammalian species were present in substantial concentrations in the peripheral blood plasma of the platypus, and the basis for the endocrine control of pregnancy is present. The degree of uterine proliferation, exhibited by the left uterus that contained the three full-term eggs in the pregnant platypus was reported by Carrick (1977) to be at least equivalent to that found in marsupials and eutherian species in the terminal stages of gestation.

It is significant that the apparently-functional ultrastructure of the full-term corpus luteum of the platypus is correlated with elevated concentrations of both progesterone and oestradiol—17 β in the peripheral blood plasma. The levels of both these hormones were reported by Carrick (1977) to be comparable to those found in certain eutherian mammals. However despite this strong circumstantial evidence for the endocrine function of the corpus luteum of the platypus, final confirmation awaits the demonstration that the luteal cells of the corpus luteum are responsible for elevated levels of progesterone and oestradiol

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—17 β in ovarian venous blood. The highest priority should obviously be given to the acquisition of this crucial information in future investigations.

TABLE 1
PROGESTERONE AND OESTRADIOL—17 β CONCENTRATIONS IN
PERIPHERAL PLASMA OF *O. ANATINUS*

STEROID (ng/ml Plasma)	Pregnant	FEMALE		Ovariectomised	MALE
		Non-Pregnant** 1	2		
Progesterone*	10.4	2.1	—	5.2	6.1
Oestradiol-17B	0.16	0.01	0.09	0.07	0.04

* The progesterone concentrations were those measured by CPBA following chromatography on Sephadex LH-20.

** Both females were adults. Animal No. 1, captured 14th February body weight 900 g; animal No. 2, captured 8th April (body weight 1182 g).

CONCLUSION

The rather unique pattern of reproduction in female monotremes is considered to have evolved as a consequence of the integration of a uterine luteal secretory phase into an otherwise fundamentally sauropsid-like mode of reproduction. The secretory products of the uterine endometrium during the luteal phase, and not the ovary, have come to constitute the major source of embryonic nutrition for the cleidoic egg.

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LEGENDS FOR FIGURES

PLATE 1:

- Fig. 1:** A newly laid egg of the platypus. The female was captured on the night of 8th September 1976 and the egg was laid between 0900 and 1500 on the 17th September.
- Fig. 2:** Photograph of the female reproductive tract of a platypus during the pre-ovulatory portion of its reproductive cycle. Note the rudimentary right ovary and slightly diminished size of the right Fallopian tube and the right uterus. Magnification x 0.9.

PLATE 2:

- Fig. 3:** Ovarian follicle of a platypus at an early stage of vitellogenesis during the breeding season. Note the lack of an antrum and the presence of a thick zona pellucida, Z.P. FC, follicle cell; VM, vitelline membrane; YP, yolk platelet (yolk sphere). Magnification X1500.
- Fig. 4:** Advanced stage of vitellogenesis in a large ovarian follicle (2 x 3.2mm) of a platypus (as for Figure 3). ZP, zona pellucida; VM, vitelline membrane; FC, follicle cell; YP, yolk platelet (yolk sphere). Magnification X1500.

PLATE 3:

- Fig. 5:** Electron micrograph of the precursors of the mucoid coat (MCP) of a pre-ovulatory platypus, within a non-ciliated secretory cell from the isthmus region of the Fallopian tube during the breeding season. Magnification X29,800.

PLATE 4:

- Fig. 6:** The role of the secretions of the monotreme oviduct with respect to the egg. This diagram is based on information from the papers of C. J. Hill (1933, 1941) and J. P. Hill (1933). The scale line refers only to the diameter of the vitellus.

PLATE 5:

- Fig. 7:** Light micrograph of the egg shell that invested the fully developed intra-uterine embryo of the platypus collected by the authors. The shell was lined by a strongly sulphated layer of glycoprotein (arrowed). BS, basal layer; R, rodlet layer; M, matrix layer. Magnification X860.
- Fig. 8:** Transmission electron micrograph showing the structure of the fully formed egg shell of the echidna. The shell is lined by a glycoprotein layer (arrowed). BS, basal layer; R, rodlet layer; M, matrix layer. Magnification X11,400.
- Fig. 9:** Scanning electron micrograph of the outer surface of the egg shell that invested the fully developed intra-uterine embryo (as for Figure 7). M, shell matrix. Magnification X2,200.

PLATE 6:

- Fig. 10:** Electron micrograph showing the non-ciliated secretory cells of a tubal gland of a post-ovulatory platypus during the breeding season. The cytoplasm of the secretory cells was packed with the presumptive precursors of the basal layer of the egg shell (arrowed). The tissue was obtained from the lower third of the Fallopian tube. Magnification X6,500.

PLATE 7:

- Fig. 11:** Electron micrograph showing portion of a uterine endometrial gland from a pre-ovulatory platypus (4mm-4.5mm ovarian follicles). Note that ciliated cells (CC) were present as well as non-ciliated secretory cells (SC). Shell precursors (arrowed) as well as presumptive nutritive material, found in apical domes (AD), were simultaneously present.

PLATE 8:

- Fig. 12:** Electron micrograph of luteal cells from the corpus luteum of the platypus with the full-term intra-uterine eggs collected by the authors. ERs, smooth endoplasmic reticulum; MT, mitochondria; IC, intercellular space; G₁, membrane bound granules; N, nucleus. The arrow indicates the probably disaggregation of a granule in the intracellular space. Magnification X16,800.

PLATE 1:

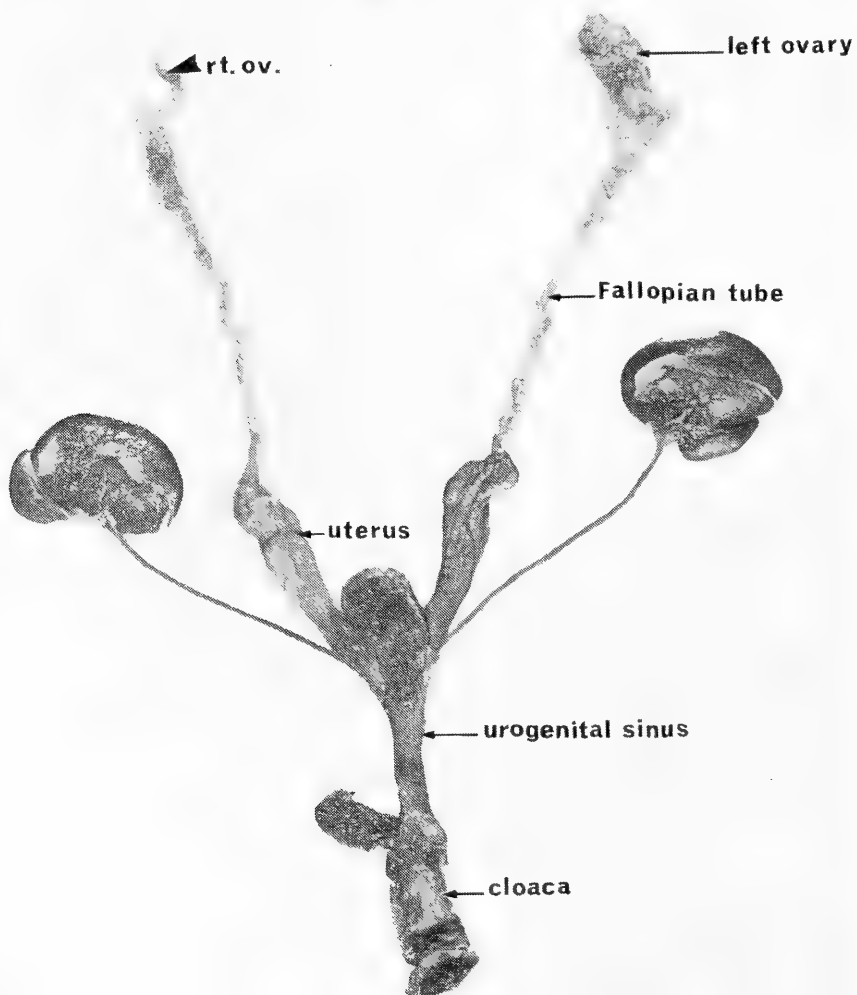
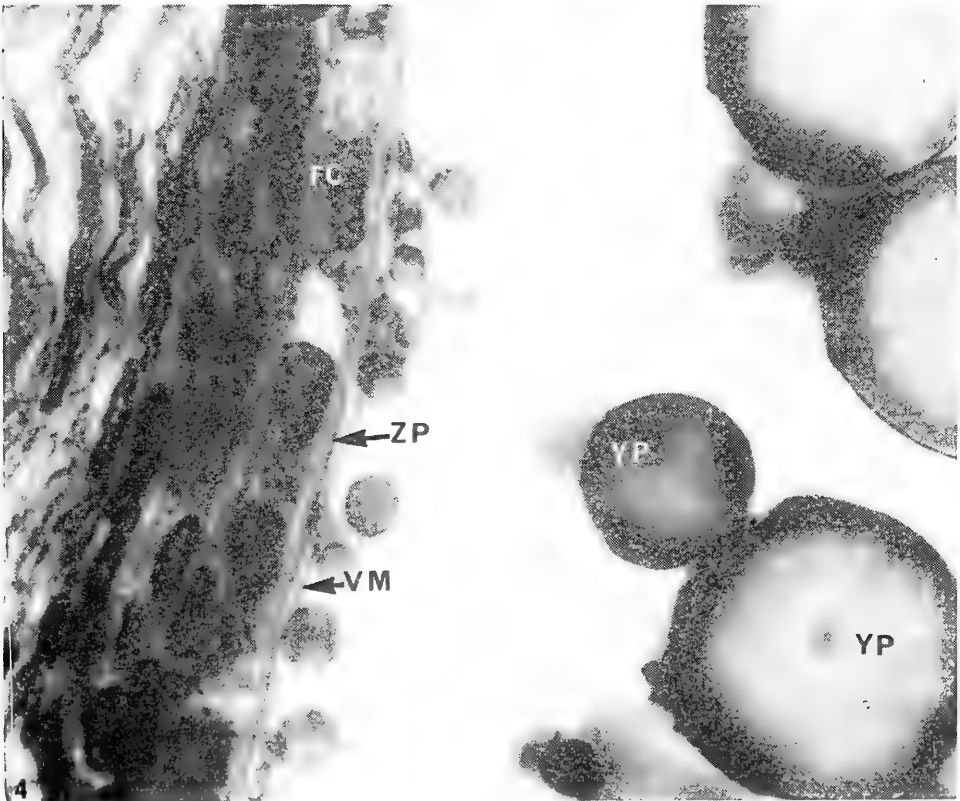
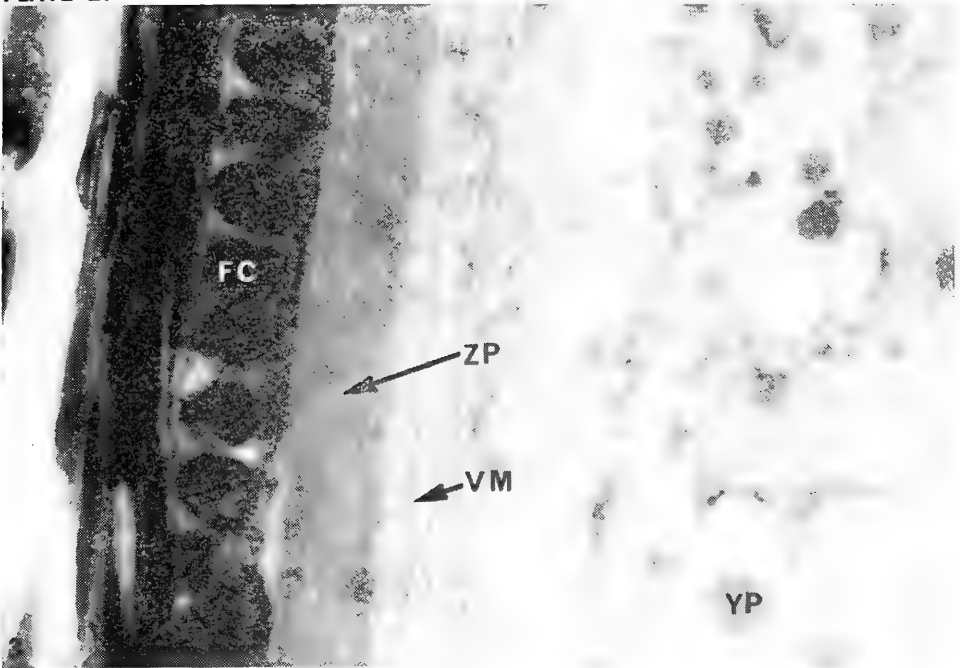


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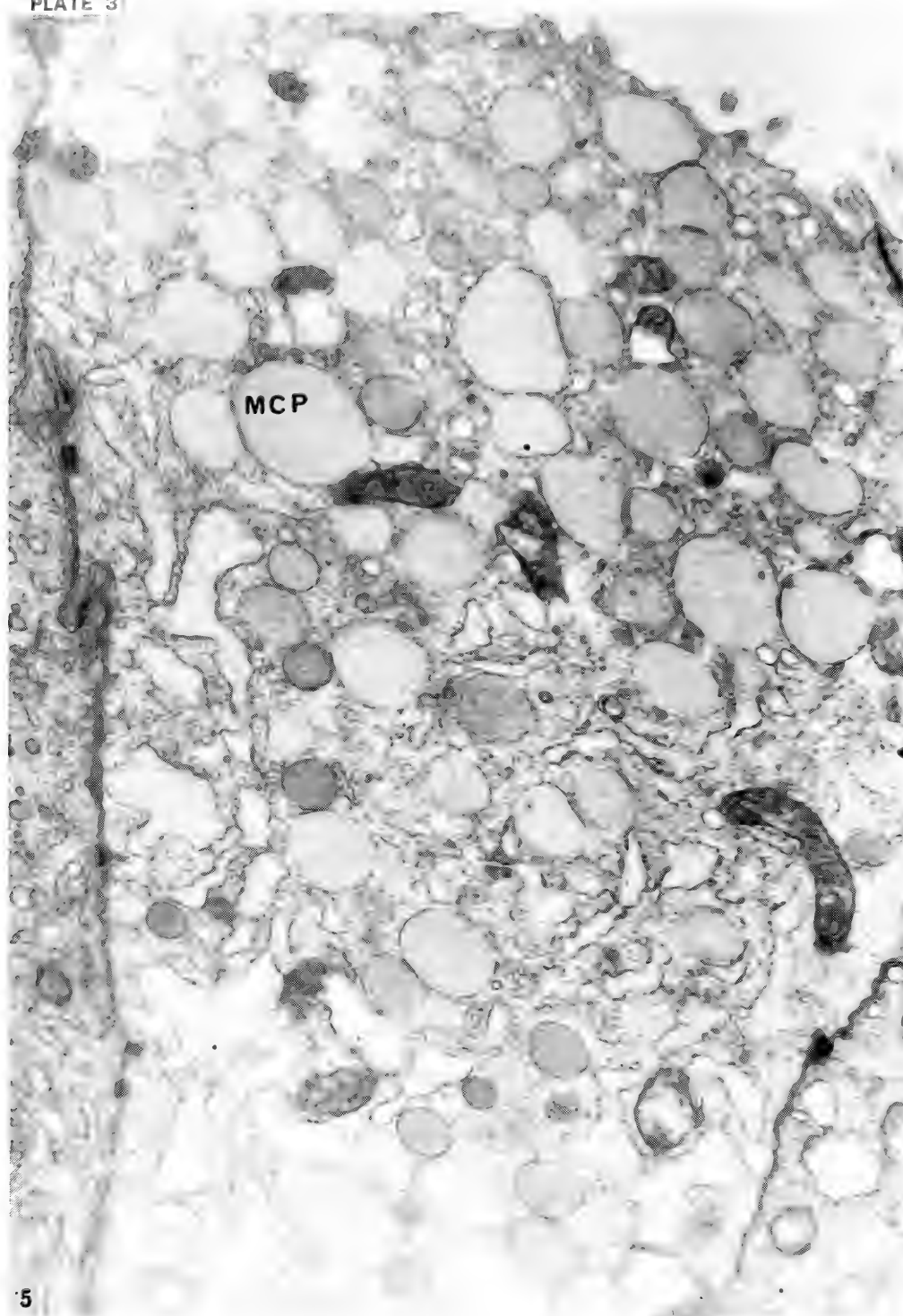


PLATE 4:

ROLE OF THE SECRETIONS OF THE MONOTREME OVIDUCT WITH
RESPECT TO THE EGG

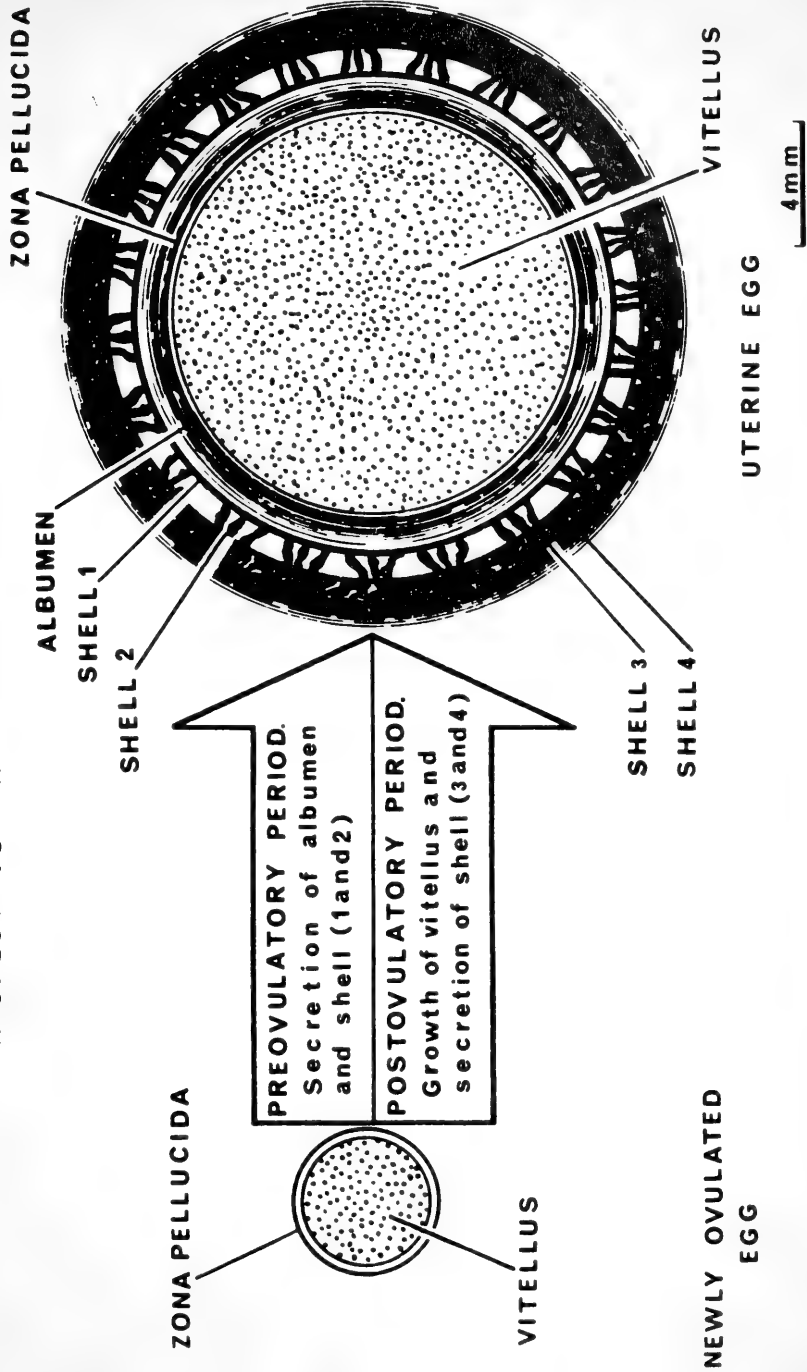


PLATE 5

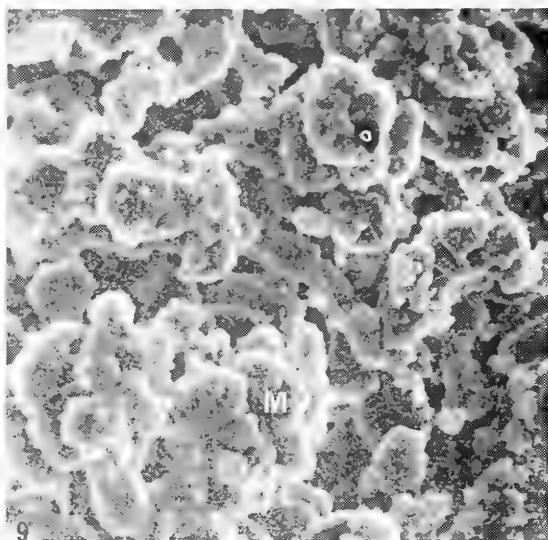
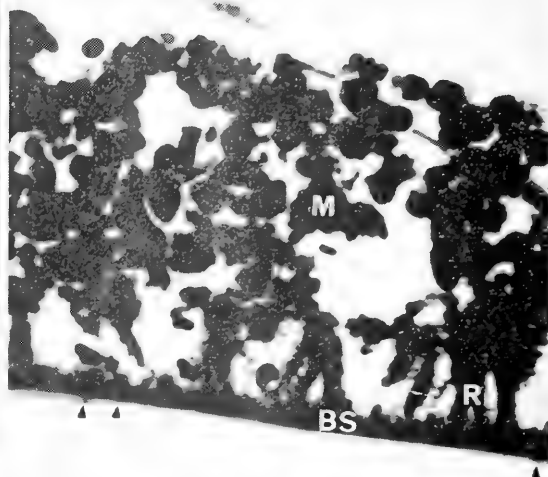
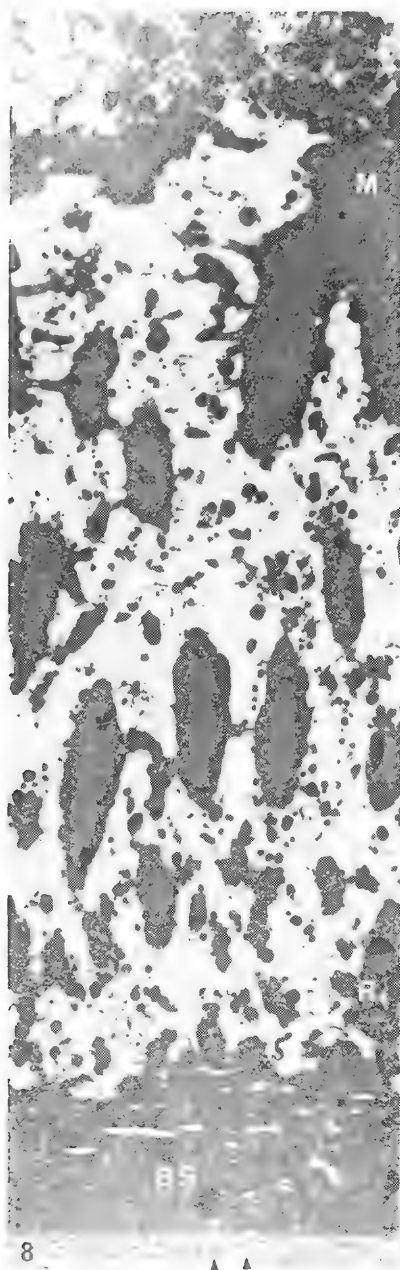
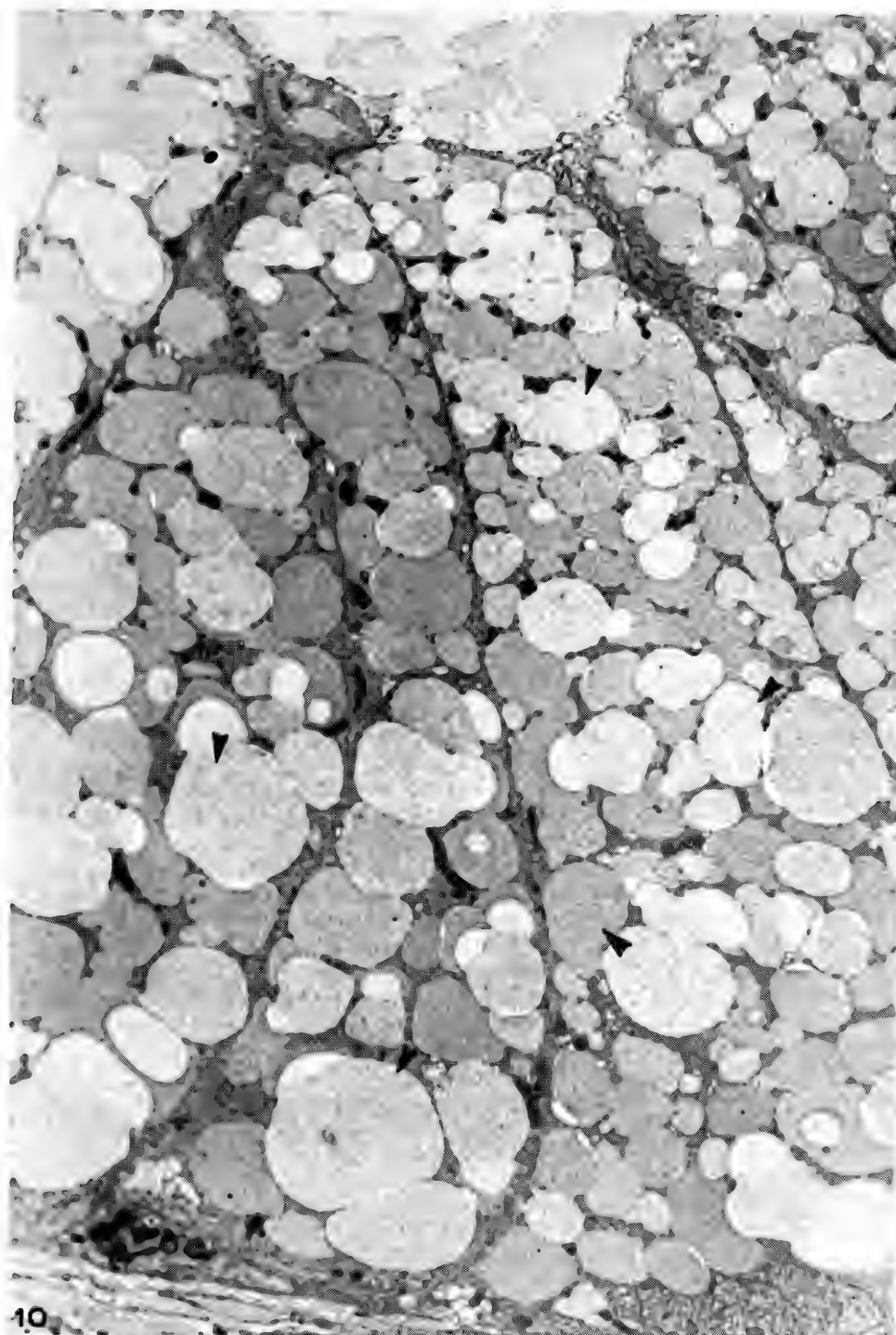


PLATE 6:



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PLATE 7.

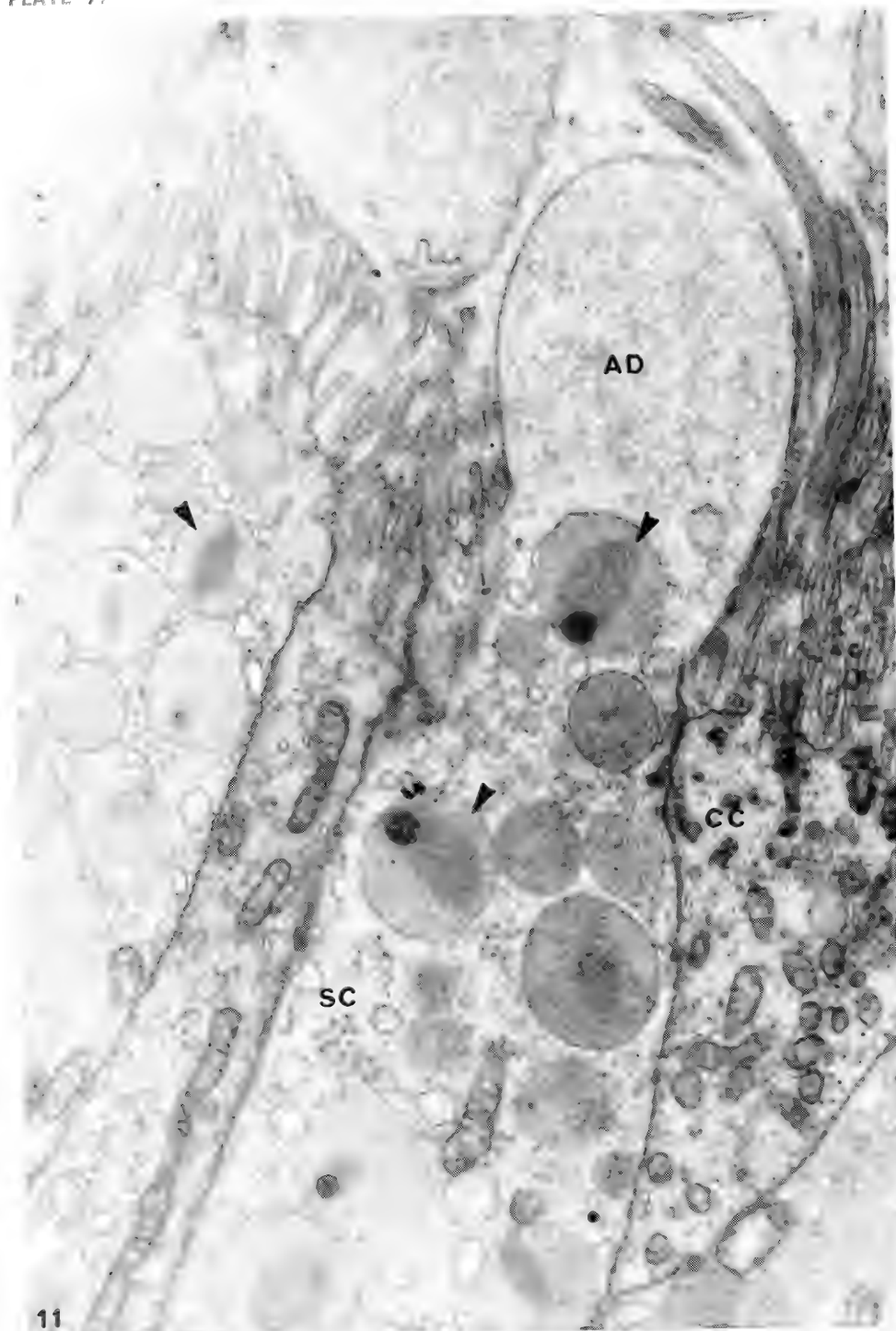
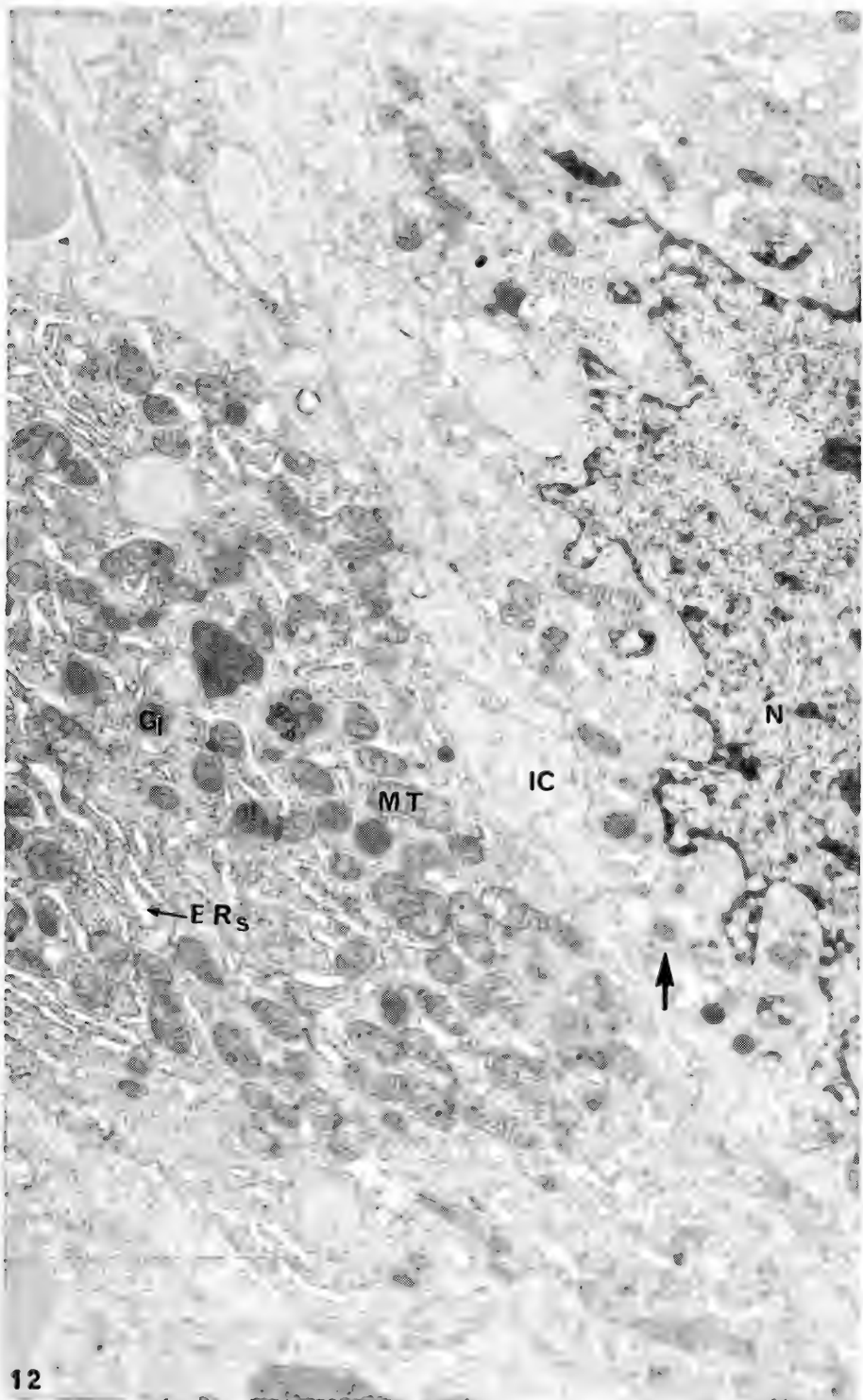


PLATE 8:



ABSTRACTS OR TITLES ONLY OF FURTHER PAPERS PRESENTED TO THE
SYMPOSIUM ON MONOTREME BIOLOGY.

BAGGETT, H. A. (Dept. of Anatomy, University of Western Australia, Nedlands, 6009)
FUNCTIONAL MORPHOLOGY OF THE TONGUE OF ECHIDNA (*TACHYGLOSSUS ACULEATUS*).

BOHRINGER, Ros (School of Anatomy, University of N.S.W., Kensington, 2033) THE
BILL OF THE PLATYPUS (*ORNITHORHYNCHUS ANATINUS*).

The role of the bill of the platypus as an important peripheral sensory organ was first proposed by the early naturalists who observed that the animal relied on tactile information from the bill during underwater feeding and navigation. In the present study the structure and distribution of peripheral nerve terminals within the bill, and the regions of the central nervous system to which these terminals projected, were examined using standard anatomical methods. In addition, the region of the cerebral cortex devoted to tactile inputs from the bill was mapped using neurophysiological techniques.

The investigations revealed that the bill, particularly its upper border, was densely innervated and that remarkably large regions within the central nervous system were devoted to inputs from the bill.

BRATTSTROM, B. H. (Dept. of Biology, California State University, Fullerton, Cal. 92634, U.S.A.) SOCIAL BEHAVIOUR OF THE ECHIDNA, *TACHYGLOSSUS ACULEATUS*: AN ENERGETIC AND EVOLUTIONARY PERSPECTIVE.

My observations on the social behaviour of the echidna have already been presented (Brattstrom 1973). In the years following that study I have published on various aspects of reptilian behaviour, on the evolution of social behaviour in reptiles, and on the fantastic learning ability of lizards (Brattstrom 1971, 1974, 1978). Based on these studies and on other studies on temperature regulation in reptiles and amphibians, I want to take this opportunity of making some remarks on the energetic and evolutionary aspects of reptilian and echidna social behaviour.

It is clear from current studies on vertebrate behaviour and thermoregulation that:

(1) Much of animal behaviour is innate (genetically fixed), yet a great deal is learned. If given the right reinforcers and task, all vertebrates can learn some tasks well.

(2) Some aspects of social behaviour may have a genetic basis (displays, courtship, territory, hierarchy), while other aspects are learned. There are also, however, strong resource related determinates of social behaviour (food availability, stability of the environment, sleeping and breeding places) which cause behaviour to be, for example, co-operative, territorial, and/or hierarchical.

(3) Population density can also affect the type of social behaviour that occurs. With an increase in population numbers (or an increase in density), aggressive interactions increase and behaviour may switch from territory to hierarchy. This may affect the reproductive behaviour or physiology of the animals that are crowded (number of young or eggs, intrauterine mortality) and change predator numbers and hunting strategies.

(4) Fighting and complex aggressive displays are energetically expensive and risky. Displaying animals are exposed to predators. Injured animals may die and reduce the availability of strong genetic contributors to the population. The energetic cost of fighting is expensive, especially to reptiles that may be forced into anaerobic respiration and thus have to spend hours repaying their oxygen debt (Bennett 1972, Bennett and Licht 1972).

(5) Fighting and complicated displays seldom occur in social interactions (often less than in 10 per cent of all male-male interactions, and then usually only between the top

1 to 3 males). Most animals in any given species know their social position (either from genetic clues or learned behaviour) and simple cues (size, colour, odours, simple gestures, bobs, waves) are used by subordinate individuals to indicate submission or avoidance. (Most animals "cop out" and do not engage in energetically expensive or risky social interactions. For example, bearded dragons wave or show a low posture, echidnas use "avoids"). Echidnas spend very little of their energy engaged in the expensive behaviours of fighting and aggression.

(6) Behaviour observed in the laboratory or other crowded conditions, allows the observer to see many if not all possible postures, positions, behaviour, and social interactions that may be in the behavioural make-up of any given species. It does not mean that the animal has to, or does utilise these behaviours in the wild, only that they are available if it needs them.

(7) Animals survive. Species survive. Each uses its evolutionally accumulated anatomy, physiology, and behaviour to cope with its surviving and reproducing. All the behavioural or physiological mechanisms that an animal species needs are just the ones it has to have to allow its survival. Others are unnecessary and energetically expensive. Each animal species in its habitat and niche will therefore have those aspects of its behaviour and physiology that allow it to cope, survive, and reproduce in that habitat and niche. This physiology and behaviour may be simple or complex and/or unique. This information, however, does not let us make remarks as to whether any given species is primitive, generalised, or advanced, but only that these are the aspects of its life that it has for survival and reproduction in its specific situation.

Echidnas are unique and uniquely echidnas! They survive, reproduce, and learn. They have reptilian as well as mammalian aspects of their anatomy, physiology, and behaviour. Basically and essentially, however, they are echidnas and adapted for survival and reproduction in their habitat and niche. It is only when selection, changing climates and environments, mutation, inbreeding, resource limitations, or human interference occurs, that the evolutionary mechanisms for survival may fail and the animal species becomes extinct. Echidnas have apparently survived for a long time.

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- HOSKEN, R. W. and B. BOETTCHER (Dept. of Biological Sciences, Univ. of Newcastle, N.S.W. 2308) FIXATION OF FUNCTIONALLY NON-EQUIVALENT HAEMOGLOBINS IN THE ECHIDNA POPULATION.
- HUME, I. D., E. C. BIRNEY and R. JENNESS (Dept. of Biochemistry and Nutrition, University of New England, Armidale, N.S.W. 2350) ASCORBIC ACID SYNTHESIS IN MONOTREMES: EVOLUTIONARY IMPLICATIONS.
- Murtagh, Carolyn E. (School of Biological Sciences, Macquarie University, North Ryde, N.S.W. 2113) THE CYTOGENETICS OF MONOTREMES.

The monotremes have a unique cytogenetic system involving a chain of chromosomes during first division of meiosis in all 3 genera. The echidna has $X_1X_1X_2X_2$ ♀ / X_1X_2Y ♂ sex chromosome constitution and the platypus has XX ♀ / XY ♂. In males these sex chromosomes are incorporated into the chain together with some autosomes. Unpaired autosomes corresponding in number to those believed to be in the chain multiple are seen amongst the mitotic chromosomes of male and female echidna and platypus. There is a also considerable chromosomal polymorphism. Ref: Murtugh, C. E. (1977), *Chromosoma* (Berl.) 65, 37-57..

Pidmore, P. A. (Dept. of Zoology, Monash University, Clayton, Vic. 3168) NON-TERRESTRIAL LOCOMOTION AND EVOLUTION IN MONOTREMES.

Monotremes are frequently described as locomotively primitive mammals. However, cineradiographic and cinegraphic studies of locomotion in the group suggest that monotremes are highly specialised for fossorial locomotion.

Monotremes and certain insectivores of the family Talpidae constitute the only living mammals which employ a 'lateral-thrust' method of burrowing. Lateral-thrust burrowing seems to be preadaptive to a semi-aquatic life-style in which the forelimbs provide propulsion.

A number of monotreme anatomical and physiological features which are often regarded as primitive or peculiar to monotremes are probably in fact fossorial adaptations.

TEMPLE-SMITH, P. D. (Anatomy Dept., Monash University, Clayton, Vic. 3168). THE CRURAL SYSTEM IN MONOTREMES.

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Early Development of the Australian Green Hyliid Frogs

Litoria chloris, *L. fallax* AND *L. gracilentia*

GRAEME F. WATSON AND ANGUS A. MARTIN

Department of Zoology, University of Melbourne, Parkville, Vic. 3052.

ABSTRACT

The life histories of *Litoria chloris*, *L. fallax* and *L. gracilentia* are described and shown to conform with the developmental pattern typical of Australian hylids.

INTRODUCTION

The life histories of the Australian Hylidae are poorly known. The only comprehensive life history studies of Australian hylids are those of *Litoria verreauxi* (Anstis, 1976), the *L. nannotis* species group (Liem, 1974), *L. jervisiensis* (Martin and Littlejohn, 1966), *L. burrowsi* (Martin, 1967b), *L. peroni* and *L. tyleri* (Martin *et al.*, 1979), and the *L. citropa* group (Tyler and Anstis, 1975). Tyler and Davies (1978) summarize the available information on Australian hylid life histories. Apart from the intrinsic interest of studies of life history patterns, they may also provide evidence bearing on relationships and phylogeny (Martin, 1967a, b; Martin and Watson, 1971; Watson and Martin, 1973). With this in mind we have been accumulating information on Australian hylid life histories for several years. The present account is of three species whose life histories were previously unknown: *Litoria chloris* (Boulenger), *L. fallax* (Peters), and *L. gracilentia* (Peters). The joint treatment of these three forms is not intended to imply any relationship; in their recent paper on species groupings within *Litoria*, Tyler and Davies (1978) placed *L. chloris* and *L. gracilentia* together in the *L. aruensis* group and *L. fallax* in the *L. bicolor* group.

METHODS

For *L. fallax* and *L. gracilentia*, amplexant pairs were collected in the field and placed in plastic containers with approximately 10 cm of pond water and

some grass stems for transport to the laboratory. In each case oviposition occurred in the enclosure. On return to the laboratory the embryos were reared in a constant temperature room ($20 \pm 0.5^\circ\text{C}$). Eggs of *L. chloris* were obtained from an amplexant pair maintained in laboratory terrarium in the Department of Zoology, University of Adelaide. Embryos were reared in a constant temperature room ($27 \pm 1.0^\circ\text{C}$). Samples of embryos and larvae were fixed in Tyler's fixative (Tyler, 1962) at irregular intervals. All measurements, drawings and descriptions are based on preserved material. Measurements were made using an ocular micrometer in a stereoscopic microscope, or vernier calipers reading to 0.05mm. Drawings were made by accurate tracing of enlarged photographs. Other techniques used

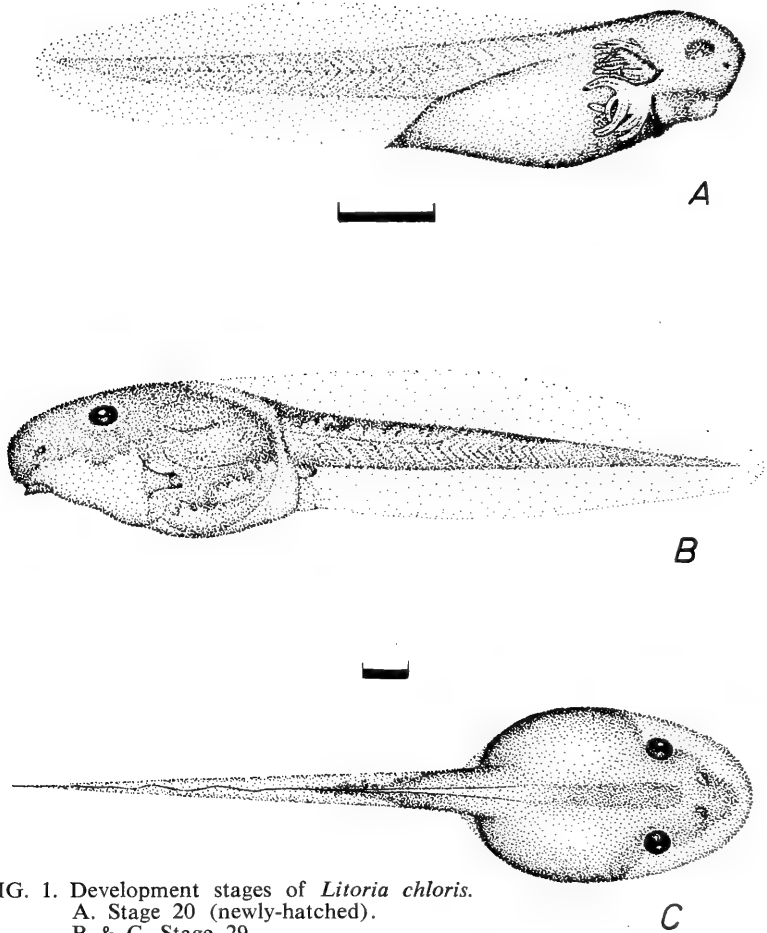


FIG. 1. Development stages of *Litoria chloris*.
A. Stage 20 (newly-hatched).
B & C. Stage 29.
The bar in each case represents 1 mm.

follow those of Martin and Littlejohn (1966), and developmental stages were classified according to the table of Gosner (1960).

RESULTS

LITORIA CHLORIS

MATERIAL:— A recently-laid clutch of eggs was obtained on 25 February, 1976, from a captive pair originally collected at Warrie N.P., Springbrook, Qld.

EGGS:— Oviposition was not observed nor could an accurate estimate of the number of eggs be obtained. Eggs were laid either singly or in very small clumps (5-15 eggs), loosely attached to submerged twigs. There is little colour differentiation between animal and vegetal poles with the former being mid-brown and the latter lighter brown. Each egg is surrounded by a poorly defined jelly capsule which lacks clear layers. The dimensions (mean and range) of six embryos in early cleavage (stage 9) were: embryo diameter, 1.65 mm (1.58-1.73); capsule diameter, 4.3 mm (3.8-4.7).

PRE-HATCHING EMBRYOS:— Early embryonic stages were not studied. The first series of embryos was preserved at 0830 hours on 27 February at stages 18-19. Their total length was about 5.3 mm. There were bulges marking the positions of the visceral arches; and optic bulges and ventral suckers were clearly visible. The overall colour was light brown with a paler yolk sac.

POST-HATCHING EMBRYOS:— Hatching began late on 27 February when the embryos were at stage 20. An embryo preserved at 0900 hours on 28 February is shown in Figure 1A. Its total length was 7.4 mm. Three pairs of external gills were present each with numerous branches. Ventral suckers were still present and the tail fin was well developed. The overall colour was mid-brown.

LARVAE:— Limb bud development began on 2 March; one larva was preserved at stage 26. The following day the larvae were at stage 29 (Figs. 1B and 1C). Pigmentation was light, the overall colour being pale brown, and the coils of the intestine were clearly visible through the body wall (Fig. 1B). The spiracle was situated below the midline on the left side and the anus opened to the right of the tail fin. The mouth disc (Fig. 2B) had a $\frac{1}{1}-\frac{1}{2}-\frac{1}{1}$ formula (see Martin, 1965, for explanation) and well-developed horny jaws. The papillary border was well developed and extended around the sides and back of the mouth disc. The dimensions of a stage 29 larva were: total length 15.9 mm; tail length 10.1 mm. The largest larva was at stage 39 and had a total length of 50.3 mm and a tail length of 34.7 mm.

METAMORPHOSIS:— Three individuals completed metamorphosis on 5 April. The newly-metamorphosed juveniles had body lengths of 16.3, 14.8 and 13.0 mm.

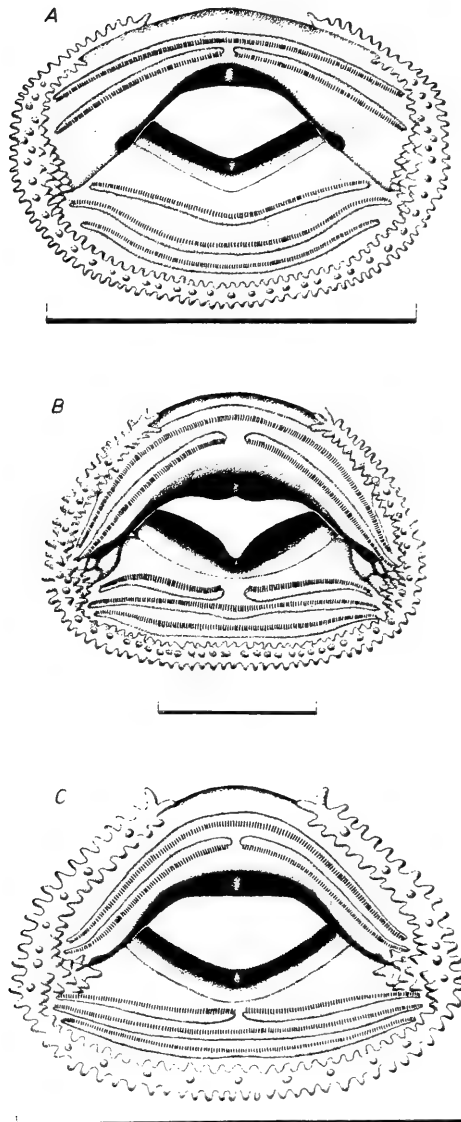


FIG. 2. Larval mouth discs at stages 27 to 29 of:
A. *Litoria fallax*,
B. *Litoria chloris*, and
C. *Litoria gracilentia*.
The bar in each case represents 1 mm.

The colour in preservative was pale brown and the general features of the juvenile resembled those of the adult (see description in Moore, 1961). All remaining specimens were preserved on 5 April.

LARVAL LIFE SPAN:— At 27°C, embryonic and larval development were completed within 41 days.

LITORIA FALLAX

MATERIAL:— A single clutch of eggs was obtained from an amplexant pair collected at Palm Grove (near Gosford), New South Wales, on 18 December 1968.

EGGS:— Oviposition was not observed. A total of 263 eggs was laid, in discrete bundles each containing 40 - 50 eggs, loosely attached to grass stems. The animal hemisphere was black and the vegetal hemisphere creamy white; each egg had a double jelly capsule. The dimensions (mean and range) of 10 embryos in early cleavage (stage 8) were: embryo diameter, 1.00 mm (0.98 - 1.03); inner capsule diameter, 1.28 mm (1.24 - 1.32); outer capsule diameter, 3.22 mm (2.80 - 3.60).

PRE-HATCHING EMBRYOS:— Early embryonic stages were not studied. The first series of embryos was preserved on 20 December, 1968, in stage 18. Their total length was about 3.2 mm. There were bulges marking the positions of the visceral arches; and optic bulges, auditory vesicles, pronephric swellings and ventral suckers were clearly visible. The overall colour was light brown, with the yolk sac creamy yellow. A further seven embryos were preserved on 23 December, when they were at stage 20 (Fig. 3A). The mean total length was 4.71 mm (range 4.44 - 5.06). Two pairs of external gills were present, the anterior pair possessing four branches and the posterior pair two. The ventral suckers were still present. The tail fin was well developed and extended along the back almost to the head. The overall colour remained light brown.

POST-HATCHING EMBRYOS:— Hatching began on 24 December, when the embryos were entering stage 21. The only marked difference from a stage 20 embryo was that the cornea was clear. The external gills were still present. On 26 December the embryos were at stage 25. The operculum was complete, with a fully developed spiracle, and the ventral suckers were still present. The mean total length was 5.43 mm (range 5.06 - 5.76).

Stage 25 was of relatively long duration, and lasted until the end of January 1969. During this stage the ventral suckers disappeared, the anal tube opened, and the mouth disc differentiated. Two stage 25 embryos preserved on 3 February 1969 have total lengths of 6.91 and 8.32 mm.

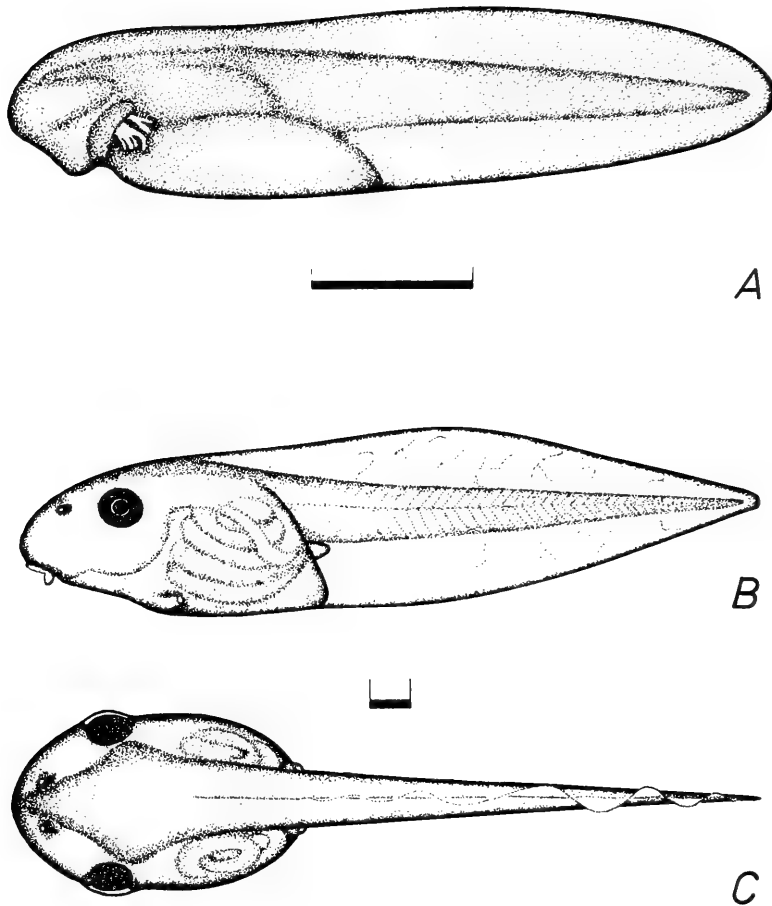


FIG. 3. Development stages of *Litoria fallax*.
 A. Stage 20.
 B & C. Stage 29.
 The bar in each case represents 1 mm.

LARVAE:— Limb bud development was first observed on 3 February when two larvae were preserved at stage 27; their total lengths were 11.15 and 12.40 mm. On 28 February two larvae were preserved at stage 29 (Fig. 3B and C). Pigmentation was very light, the overall colour being pale yellowish brown, and the coils of the intestine were clearly visible through the body wall. The fins were clear except along some of the blood vessels. There were scattered pigment spots along the dorsal edge of the tail musculature and over the cranium. The spiracle

was situated low on the left side of the body and the anus opened to the right of the tail fin. The mouth disc (Fig. 2A) had a $\frac{1}{3}$ formula.

The papillary border extended around the sides and back of the mouth disc, and was broadened along the lateral margins. The dimensions of the two stage 29 larvae were: total length, 17.7 and 18.0 mm; tail length, 10.8 and 10.8 mm respectively.

On 27 March 1969 the larvae had reached stage 31. Two of these individuals had total lengths of 21.7 and 21.9 mm. Three larvae were preserved on 14 April when they had reached stage 41. Their body dimensions were: total length, 31.3, 32.1 and 32.4 mm; tail length, 20.5, 22.1 and 21.4 mm respectively.

METAMORPHOSIS:— Three individuals metamorphosed between 15 and 29 April 1969. These juveniles had body lengths of 10.9, 11.4 and 12.1 mm. The colouration and skin texture of the juveniles were similar to those of adults (see description in Moore, 1961).

LARVAL LIFE SPAN:— At 20°C, the larval life span extended from 118 to 132 days.

LITORIA GRACILENTA

MATERIAL:— Some eggs were obtained from a nearly-spent female collected in amplexus from a roadside pond 6.4 km SW of Nerang, Qld. on 9 November 1972.

EGGS:— Oviposition was not observed. So few eggs were laid that none were preserved. An adequate description of the egg mass was likewise impossible; the few eggs laid were loosely attached to grass stems.

PRE-HATCHING EMBRYOS:— Early embryonic stages were not studied. The first series of embryos was preserved on 11 November at stage 19. Their total length was about 3.7 mm. The tail fin was moderately well developed and bulges clearly marked the positions of the visceral arches; olfactory pits and ventral suckers were visible. The overall colour was mid-brown with a creamy yolk sac.

POST-HATCHING EMBRYOS:— Hatching began on 12 November when the embryos were at stage 20. Figure 4A shows an embryo preserved at this time. Its total length was 5.12 mm. Two pairs of external gills were present, the anterior pair having 5-6 branches and the posterior pair 3-4. The tail fin was very well developed and extended dorsally to the eye rudiment. Ventral suckers were well developed. The overall colour was pale brown with scattered dark pigment spots on the dorsum. On 13 November embryos had reached stage 24-25. Total lengths of two individuals preserved at this time were 6.25 and 7.19 mm. At this stage the body wall was transparent revealing the coils of the yolk-filled intestine. The

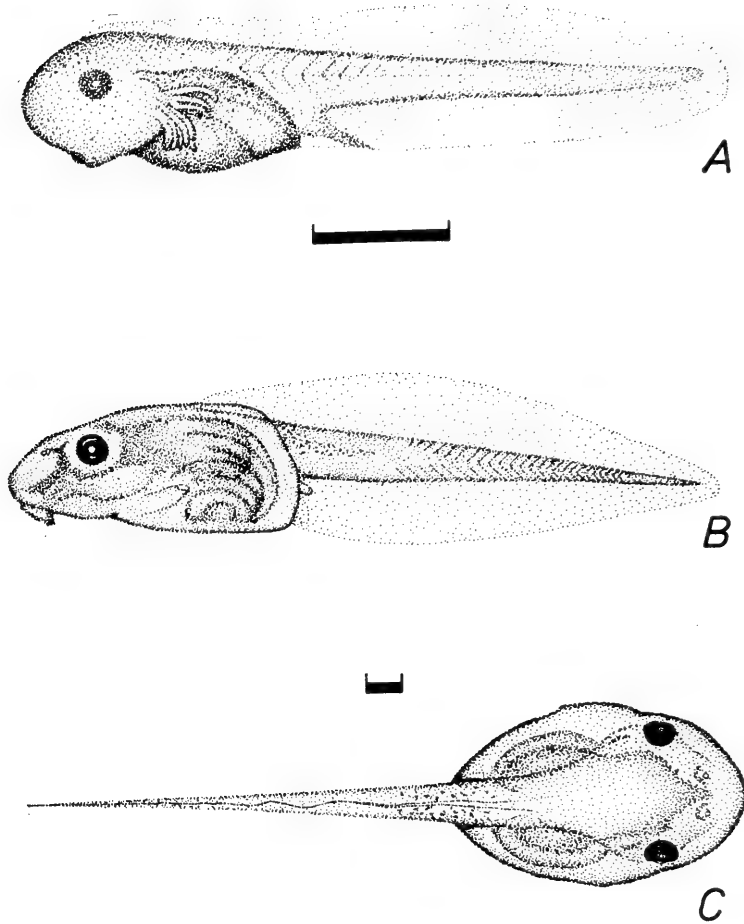


FIG. 4. Development stages of *Litoria gracilentia*.
A. Stage 20 (newly-hatched).
B & C. Stage 28.
The bar in each case represents 1 mm.

mouth had differentiated but the anus was not yet open. Ventral suckers were still present. Colour was pale brown with extensive pigment spots across the dorsum and tail musculature.

LARVAE:— The first larvae available for examination were preserved on 13 December, when they were at stage 28 (Figs. 4B and C). Dimensions of the two larvae were, total length 19.14 and 20.48 mm and tail length 11.28 and 12.00 mm

respectively. The larvae were mid-brown with dark pigmentation of the dorsum, the upper portion of the intestinal peritoneum, and the anterior tail musculature. The ventral coils of the intestine could be seen through the body wall. The spiracle was placed ventro-laterally on the left side and the anus opened to the right of the tail fin. The mouth disc (Fig. 2c) had a $\frac{1}{1} \frac{1}{2} \frac{1}{1}$ formula. The disc was bordered on its lateral and posterior margins by well developed, protruding rows of papillae.

The largest larva in this series was preserved on 9 March, 1973, at stage 37. Its dimensions were: total length 34.00mm and tail length 21.10mm. The most conspicuous difference between this individual and the stage 28 specimens was the extent of dark pigmentation. The tail fin at stage 37 had numerous large pigment spots and pigmentation was very extensive on the body and tail fin musculature.

METAMORPHOSIS:— Three individuals completed metamorphosis on 28 February 1973. These juveniles had body lengths of 11.7, 10.9 and 11.2 mm. Colouration in preservative was pale brown.

LARVAL LIFE SPAN:— At 20°C, the larval life span extended over 112 days.

DISCUSSION

As noted by Martin and Watson (1971) the life history patterns of Australian hylid frogs show remarkably little variation. The three species considered here share most of the life history characteristics typical of Australian hylids. These include aquatic oviposition, and clumped eggs, probably attached to submerged vegetation. Embryonic development and larval morphology also conform to the typical hylid pattern: well-developed external gills, a dextral anus, a sinistral, ventro-lateral spiracle, a more or less acuminate tail, and a basic 2/3 mouth formula with lateral and posterior labial papillae.

However, despite the essential conservatism of embryonic and larval characteristics in the hylids there are some noteworthy features in each of the life histories considered here. *L. chloris* is distinguished by its rate of development, which, even allowing for the difference in culture temperatures, greatly exceeds those of the other two species. This is presumably an adaptation to life in the ephemeral waters which seem to represent the typical breeding habitat of this species. Morphologically the only unusual feature of the *L. chloris* tadpole is the position of the eyes which are situated more dorsally than in the other two species, giving the tadpole a superficially leptodactylid-like appearance.

The mouth of *L. fallax* is unusual amongst Australian hylids in having three complete rows of lower labial teeth. In most Australian species the first lower row is divided.

L. gracilentia differs least from the usual hylid life history pattern, being typical of species occurring in permanent, lentic waters. It is interesting to note that while *L. chloris* and *L. gracilentia* are apparently closely related (Tyler & Davies, 1978), their patterns of larval development show adaptations to strikingly different environmental conditions.

ACKNOWLEDGEMENTS

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Some Observations on the Spawning and Development of the Mitchellian Freshwater Hardyhead *Craterocephalus fluviatilis* McCulloch from Inland Waters in New South Wales

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ABSTRACT

Mitchellian Freshwater Hardyhead were induced to spawn in a pond at Narrandera and observations on their breeding requirements and embryonic development were recorded. They had an extended breeding season from mid October to mid February according to the state of their gonads, when pond temperatures were at or above 24.7°C at the surface and 23.6°C at the bottom. Eggs were successfully stripped from fish but not fertilised when surface temperatures were 27.8°C and bottom temperatures 24.6°C. Water continually flowed through the pond where a successful breeding occurred on 12 December 1968. Two fertilised eggs were found 17 hours after fertilisation (estimated), when they measured 1.32 and 1.34 mm in diameter. Unfertilised eggs increased in mean diameter from 1.29 to 1.46 mm during water hardening.

The eggs possessed a thick chorion covered with filamentous adhesive strands and were demersal, spherical, fairly transparent, had 5-11 oil globules clustered together and had a small perivitelline space. Larvae were approximately 3.4 mm in length at hatching and possessed black pigmented eyes and numerous melanophores on the body. Fish grew from 27 mm to 46 mm in 18 months in aquaria. The ovaries and testes were single-lobed and during the breeding season the male fish were golden coloured ventrally and the females were silvery. The latter also had black pigment showing around the vent from the black mesovarium. In *Craterocephalus fluviatilis* the gonosomatic index for females varied from 0.4-13.1 and ripe ovaries possessed 20-107 large-sized ova (over 0.90 mm in diameter) and 459-2200 medium-sized ova (0.10-0.90 mm in diameter). The gonosomatic index for males varied from 1.2 to 7.2. In a second species from the area, *C. eyresii*, the gonosomatic index reached 17.4 and ripe ovaries possessed 73-144 large-sized ova (over 0.90mm in diameter) and 1132-1701 medium-sized ova (0.10-1.90 mm in diameter).

INTRODUCTION

The Mitchellian Freshwater Hardyhead *Craterocephalus fluviatilis* McCulloch, often called the Freshwater Silverside or Line-eye, belongs to the family Atherinidae. According to Munro (1956-62) nine other Australian species are included in this genus and one additional species has been described since then by Ivantsoff and

TABLE 1

COLLECTIONS OF MITCHELLIAN FRESHWATER HARDYHEAD

Date	Locality	Number	Remarks
<i>C. fluviatilis</i>			
21.viii.59	Darling River above Bogan River	8	4 males, 1 female
2.xii.59	Darling River below Bourke Weir	3	—
17.i.60	Barwon River, near Brewarrina	7	5 females, 1 juv.
20.i.60	Bokhara River, S. of Bokhara	2	1 male, 1 spent female
27.ii.60	Murray River, Euston (fish ladder)	4	3 males, 1 female ripe
23.iii.60	Bogan River, Tarcoon	1	1 female spent
5.viii.60	Mole River Bridge, Tenterfield	14	—
6.iii.65	Below Willandra Weir	1	1 female
14.iii.65	Willow Dam	nil	—
23.iii.65	Willow Dam	nil	—
14.iii.66	Willow Dam	nil	—
12.iv.66	Willow Dam	nil	—
1.xi.66	Willow Dam	27	—
7.iii.67	Willow Dam	nil	—
3.v.67	Willow Dam	nil	—
20.v.67	Narrandera (common)	2	—
25.v.67	Willow Dam	nil	9.3—9.7°C
27.vii.67	Willow Dam	nil	Morning 9.3—11.5°C afternoon 12.0—12.8°C pH 7.6—8.4
4.ix.67	Willow Dam	nil	13.0°C
18.ix.67	Willow Dam	nil	14.7—15.0°C
2.xi.67	Willow Dam	33	—
7.xi.67	Willow Dam	41	—
23.xi.67	Willow Dam	9	21.6—22.8°C
12.xii.67	Willow Dam	1	21.2—24.0°C
16.xii.67	Willow Dam	nil	—
26.xii.67	Willow Dam	nil	—
18.i.68	Willow Dam	nil	Morning 22.0—25.2°C afternoon 23.0—28.0°C
14.ii.68	Willow Dam	nil	23.9—26.3°C (pH 9.2)
19.ii.68	Willow Dam	nil	—
4.ii.68	Lake Talbot, Narrandera	180	—
3.iii.68	Lake Talbot, Narrandera	53	—
29.iii.68	Lake Talbot, Narrandera	88	—
4.vi.68	Willow Dam	nil	—
20.vi.68	Willow Dam	3	25.0mm in length
30.x.68	Willow Dam	15	31.3—52.3mm in length
17.ii.70	Willow Dam	408	—
16.iv.70	Roach's Regulator, Narrandera	6	—
29.x.72	Lake Brewster	1	—
—	Lake Cargellico	3	—
<i>C. eyresii</i>			
25.xi.68	Euston (lagoon)	2	1 female ripe, caught amongst <i>Ludwigia</i> sp. pondweed
10.v.72	Elsmore, near Inverell	3	3 females

N.B. Where two water temperatures are given they are bottom and surface temperatures respectively.

Glover (1974). Until recently the only species recorded from the Murray Darling River system in inland New South Wales was *C. fluviatilis*; however Ivantsoff and Glover (unpublished data) found that *Craterocephalus eyresii* also occurs in this area, and Ivantsoff has identified 5 further specimens of *C. eyresii* in my personal collection, three from Elsmore near Inverell and two from a lagoon at Euston. However, out of 866 of this genus taken from the Narrandera area for breeding trials 160 specimens were examined closely and all were identified as *C. fluviatilis*.

The two species are not found at higher altitudes west of the dividing range in New South Wales, but occur patchily in lowland rivers, lakes, billabongs and swamps of the inland, generally showing preference for areas with little flow, although they may accumulate where more rapidly flowing waters enter lentic water bodies. On the occasions when they are found, they may be caught in considerable numbers (see Table 1, 17 February 1970) and seem to show little preference for either open waters or weedy areas. Regular sampling of *C. fluviatilis* is not possible because of its patchy distribution and seasonal fluctuations in numbers. Thus collection data is rather sparse. No observations on the breeding biology of any Australian species in the genus *Craterocephalus* have been described to date.

The first sample of fish collected by the author, 27 in number (Table 1), was caught on 1 November 1966 at Willow Dam which is adjacent to Barren Box Swamp, situated 22 km west-north-west of Griffith in the Riverina. This area had been chosen as a collecting site for numerous other species of forage fish (Llewellyn 1974 and 1979) and was sampled regularly, particularly during early spring and summer. However, successful catches at this site were still sporadic and relatively few in number. 408 fish were caught at a second site, Lake Talbot, on the outskirts of Narrandera, during three visits to this area in March 1968.

Due to heavy losses during catching and handling, it was difficult to stock ponds with sufficient fish for breeding trials. However, breeding occurred on three occasions and because of the paucity of breeding data on this species these observations are reported here.

MATERIALS AND METHODS

Willow Dam, where most of the collecting was carried out (34°11'S and 145°50'E) is large cumbungi swamp (*Typha* sp.). The methods and incidence of sampling and transportation of fish from Willow Dam have been outlined previously (Llewellyn, 1974, see also Table 4). Most fish at this site were caught over a 6 hour collecting period in riffle areas in the ports below the low level weirs and few were caught in adjacent weedy areas. By contrast Lake Talbot (34°45'S and 146°34'E) is an artificial lake possessing little weed. Fish were

caught in this area by using a small haul net 4.57m in length (square mesh of approximately 0.5cm sides). This method of capture was only successful when the lake was very low.

From late 1966 onwards, when the first live fish were collected at Willow Dam, unsuccessful attempts were made to keep adult fish in 90 l aquaria, and when sufficient numbers were obtained they were stocked in ponds of two sizes, one 0.11 ha in area and 183 cm deep and another 0.13 ha in area and 137 cm deep.

Between 4 and 50 adult fish were stocked in aquaria and crushed shrimp and plankton were supplied; in addition there was a heavy growth of *Spirogyra* sp. in the aquaria. However, strands of this algae were seen trailing from their anus on a number of occasions suggesting that they were eating the plant material and not the food supplied. This agrees with the findings of Ivantsoff and Glover (1974) for a closely related species *Craterocephalus dalhousiensis*, where fragments of plant tissue were found in the gut. The temperature of water in aquaria was normally at 19.0°C but was raised to 27.0°C during the breeding period (i.e. December to mid February when wild fish have mature gonads). These temperature changes did not alter the condition of the fish. pH of water during these trials varied between 7.5 and 8.6. As a result, use of aquaria was discontinued due to poor survival and condition of fish and the unlikelihood of succeeding in inducing breeding. Similar problems were experienced with *Nannoperca australis* and *Nannoperca vittata* (Llewellyn, 1974). Further attempts to breed these fish were only carried out in pond conditions.

60 fish stocked in the smaller pond prior to September 1968, all died because of a structural fault in the pond. In February 1970 this pond was restocked with 352 fish (size range 30-90 mm) caught from Willow Dam (Table 1). Unfortunately the females had finished spawning and further attempts to collect eggs and larvae were unsuccessful.

A total of 98 fish were successfully stocked into the larger pond by July 1968 (see Table 1 early 1968 catches) and a slow but steady flow of water was maintained through the pond from 21 June 1968 onwards. Samples of adult fish were taken from the pond in August, September and October (Table 2 & 3) for determination of their ovary and testis conditions. They were weighed, measured and examined for state of gonad maturation in order to determine how close they were to spawning (as described by Bodola, 1964). Ripe ovaries were preserved in Bouin's Fluid (Gatenby and Cowdry, 1928) for fecundity determinations and ova were then counted. Only large ova (above 0.90 mm) and medium sized ova (0.11-0.90 mm) were counted. Smaller ova (0.04-0.10 mm) were not counted. The gonosomatic index was determined also. All specimens of fish with ripe ovaries were treated in this way. From the state of the ovaries of samples taken on 23 October 1968, it was obvious that the spawning season was approaching rapidly. Due to

TABLE 2
BIOLOGICAL DATA ON MITCHELLIAN FRESHWATER HARDYHEADS—FEMALES

Capture Date	Weight (g)	Length to Caudal Fork (mm)	Total Length (mm)	Ovary Weight (g)	Gono-somatic Index	FECUNDITY (Nos. eggs)			Place of Collection	Comments
						Ova (0.04—0.10 mm)	Ova (0.11—0.90 mm)	Ova (above 0.90 mm)		
<i>C. fluviatilis</i>										
3.xii.69	0.7954	—	—	0.0246	3.1	—	—	—	Pond I.F.R.S.*	Large ova 1.15—1.52 mm
23.x.68	0.9805	45.4	47.1	0.1289	13.1	Numerous	976	42	" "	Large ova 1.11—1.39 mm
14.i.71	0.9219	44.5	47.5	0.0845	9.2	Numerous	1017	60	" "	—
25.viii.68	0.7793	47.3	49.4	0.0222	2.8	—	—	—	" "	Large ova 0.32—0.40 mm
17.ii.70	1.0581	52.0	55.0	0.6520	6.2	—	—	—	Willow Dam	Sample dried up.
8.i.70	—	52.0	55.5	0.0797	—	Numerous	459	20	Pond I.F.R.S.	Just spent. Could not be stripped
22.i.70	1.2356	53.0	56.0	0.1072	8.7	—	—	—	" "	Egg diameter—1.33 mm
3.ii.70	1.3782	54.0	56.0	0.1197	8.7	Numerous	589	59	" "	Ova stripped. Fish silvery in colour.
22.i.70	1.3600	54.0	57.0	0.1098	8.1	—	—	—	" "	Large ova 0.86—1.52 mm
12.iii.70	1.2470	54.0	57.0	0.0209	1.7	—	—	—	" "	—
23.x.68	2.0020	57.3	59.3	0.2165	10.8	Numerous	2200	48	" "	Sample dried up.
3.ii.70	1.6579	56.0	60.0	0.1861	11.2	Numerous	1241	107	" "	—
27.ii.60	2.2520	59.0	61.0	0.1230	5.4	Numerous	531	31	Euston-Murray River	—
18.ii.69	1.8791	59.0	62.0	0.0274	1.5	—	—	—	Pond I.F.R.S.	Large ova 0.36—0.46 mm
12.iii.70	2.7908	66.0	70.5	0.0288	0.4	—	—	—	" "	Spent
4.ix.68	2.5353	67.4	71.0	0.1114	4.4	—	—	—	" "	Large ova 0.27—0.38 mm
17.ii.70	3.2756	75.0	78.5	0.0828	2.5	—	—	—	Willow Dam	Developing ovaries
<i>C. eyresii</i>										
10.v.72	1.8630	53.0	55.0	0.2920	15.7	Numerous	1632	137	Little Valley,	Just spent, resorbing
10.v.72	1.8560	52.0	56.0	0.2640	14.2	Numerous	1132	73	Elsmore nr.	—
10.v.72	2.3550	54.0	58.0	0.4090	17.4	Numerous	1466	144	Inverell	—
25.xi.68	2.9900	62.5	65.5	0.4500	15.0	Numerous	1701	136	Euston Lagoon	Few really large ova. Large ova 1.28—1.59 mm

* I.F.R.S. Inland Fisheries Research Station at Narrandera.

the small perivitelline space in water-hardened unfertilised ova, it was almost certain that the ova would be demersal. However, both benthic and planktonic samples were taken every two days for the ensuing period in order to collect either ova or larvae (for details of the methods of sampling see Llewellyn 1974). Only two developing eggs were collected. These were kept in covered petri dishes and were photographed at regular intervals through a microscope. Temperature and time records were kept, and sketches were made to record accurate dimensions. Drawings of the various developmental stages were made with the aid of photographs. The adhesive fibres surrounding much of the egg were omitted from the drawings.

Although other ponds were stocked in 1968, late 1969 and early 1970, repeated attempts to collect further information on spawning and development in the 1969, 1970 and 1971 breeding seasons were unsuccessful.

On two occasions ripe females from ponds were stripped and attempts were made to fertilise the resultant ova with milt. These ova were measured immediately after stripping but further development did not take place.

TABLE 3

BIOLOGICAL DATA ON MITCHELLIAN FRESHWATER HARDYHEADS—MALES

Capture Date	Weight (g)	Length to Caudal Fork (mm)	Total Length (mm)	Testes Weight (g)	Gono-somatic Index	Place of Collection	Comments
<i>C. fluviatilis</i>							
27.ii.60	0.7560	40.0	42.0	0.0190	2.5	Murray River	—
8.i.70	0.6979	44.0	46.2	0.0330	4.7	Pond I.F.R.S.	Running ripe. Fish golden ventrally
2.ii.70	0.7618	45.0	48.0	0.0315	4.1	" "	—
23.x.68	1.0240	46.7	48.7	0.0720	7.0	" "	Testes parasitised. Fish golden ventrally
12.iii.70	0.7950	47.0	49.5	0.0155	1.9	" "	—
22.i.70	1.0522	48.0	51.0	0.0482	4.6	" "	Fish golden ventrally. Milt not readily extruded.
12.iii.70	1.0930	49.5	52.0	0.0190	1.7	" "	Undeveloped testes.
3.ii.70	1.0780	51.0	52.5	0.0780	7.2	" "	—
27.ii.60	1.5260	56.0	59.0	0.0180	1.2	} Murray River Euston	—
27.ii.60	1.7800	56.0	59.0	0.0390	2.2		—
22.i.70	2.8835	70.0	75.0	0.0853	3.0		Not breeding
<i>C. eyresii</i>							
25.xi.68	2.5200	60.6	63.1	0.3200	12.7	Euston Lagoon	Heavily parasitised

MITCHELLIAN FRESHWATER HARDYHEAD

As the breeding season approached, progressively developing sexual dimorphic characters were noted.

Juvenile fish were kept successfully in aquaria. Two 90 l aquaria were stocked each with six juvenile fish. In one aquarium, the mean total length of the fish stocked was 26.2 mm and the mean caudal fork length 25.1 mm. These came from a successful breeding in one of the ponds. The fish in the other aquarium had a mean total length of 22.4 mm and a mean caudal fork length of 21.2 mm and were collected from Roach's Regulator 14 km N.W. of Narrandera. These aquaria soon possessed a considerable amount of filamentous algae (*Spirogyra* sp.) which presumably acted as a source of food, and although their growth was fair their condition was never particularly good. These fish were measured periodically in order to determine their rate of growth. No displaying or breeding was observed in these fish.

RESULTS

INDUCED BREEDING

The complete record of fish collected at Willow Dam together with other incidental records is shown in Table 1. With the exception of the one large catch of 408 on 17 February 1970 (Table 1 and 4) most of the catches at Willow Dam were obtained in October and November which possibly indicates the fishes movement up the channel from Barren Box Swamp to the adjacent Willow Dam, as the breeding season approaches.

TABLE 4

WILLOW DAM—FISH CATCHES AND VISITS OVER A 5 YEAR PERIOD 1965—70
(FROM TABLE 1)

Months	J	F	M	A	M	J	J	A	S	O	N	D	Total
Number of visits	1	3	4	1	2	2	1	—	2	1	4	3	24
Number of fish caught	—	408	—	—	—	3	—	—	—	15	110	1	537
Mean No. of fish per visit per month	—	136.0	—	—	—	1.5	—	—	—	15.0	27.5	0.3	22.4

Fish taken from the large pond for examination of gonads in August, September and October 1968 showed progressive development of ovaries. On 4 September 1968 the largest oocytes measured were 0.33 mm. By 23 October 1968 the largest oocytes were 1.3 mm in diameter and many females were gravid indicating the

onset of breeding. At this time the temperature of the pond water was 20.5°C at the surface and 18.9°C at the bottom (Fig. 1) and adult fish could be sexed readily.

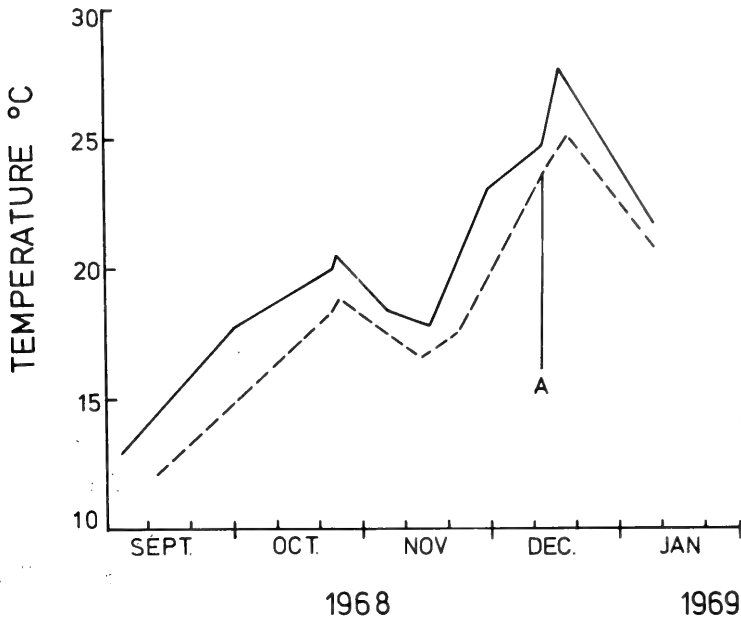


FIG. 1. Daytime pond temperatures during successful breeding between September 1968 and January 1969 (— surface temperature; --- bottom temperature).
A. Date of spawning.

Two eggs were collected in a benthic sample on 12 December 1968 when temperatures were 24.7°C at the surface and 23.6°C at the bottom (Fig. 1). Numerous attempts to collect more eggs were unsuccessful although it appeared that breeding continued for at least a month, since adult female fish remained in a reproductive state over this period.

Approximately 80 fish were still present in the large pond in spring 1969 but examination of adult fish (83-104 mm in length), sampled regularly from the pond, indicated that breeding did not occur during the 1969/70 season, although pond temperatures reached 27.8°C at the surface and 24.6°C at the bottom by 20 January 1970. No breeding colouration of males was observed. It is possible that breeding occurred during the 1970/71 season in this pond, though repeated sampling from November onwards did not reveal any eggs or larvae although coloured males were observed. However, when the pond was emptied on 26 May 1971, 13 large fish (50-90 mm in length) and 21 smaller fish (20-50 mm in length)

MITCHELLIAN FRESHWATER HARDYHEAD

were retrieved. These recoveries suggest that breeding had occurred in the previous season. Breeding success and/or survival within the pond was nevertheless poor and no doubt accounted for the difficulty in locating eggs or larvae.

Two attempts to strip the ova from females were successful, one on 19 January and the second on 3 February 1970. On the first occasion the temperature

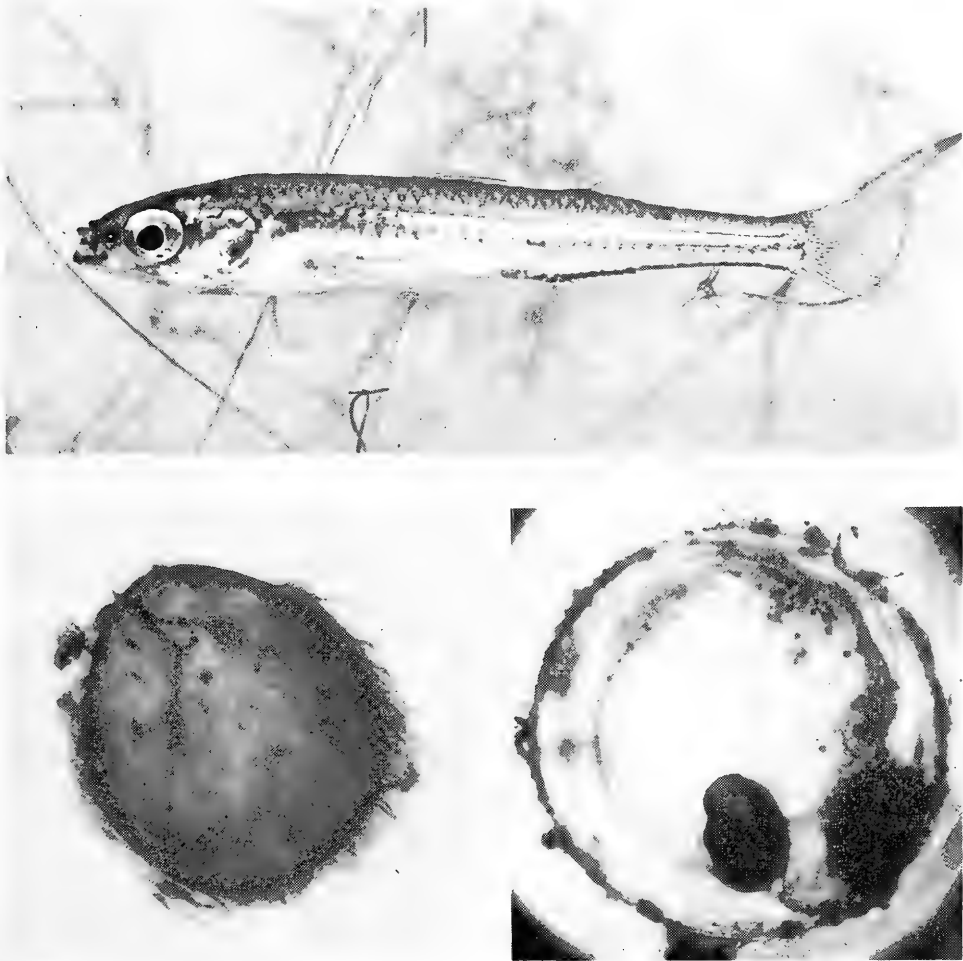


FIG. 2. (a) Adult *Craterocephalus fluviatilis*.

(b) Egg stripped from adult showing covering of adhesive filamentous strands.

(c) Photograph of egg 102 hours after collection (approximately 119 hours after fertilisation), showing well developed head with pigmented eyes and body with numerous melanophores and coiled at least once around the yolk.

of the pond water was 27.8°C at the surface and 24.6°C at the bottom. A total of 27 ova were stripped from a single fish, the first few ova being extruded very easily. On the second occasion 26 ova were stripped from a single fish. The diameter of ova from these strippings varied from 0.86-1.52 mm with a mean diameter of 1.29 mm and they were covered in stringy sticky fibres. An attempt to fertilise these ova with milt from a male which was not fully ripe proved unsuccessful.

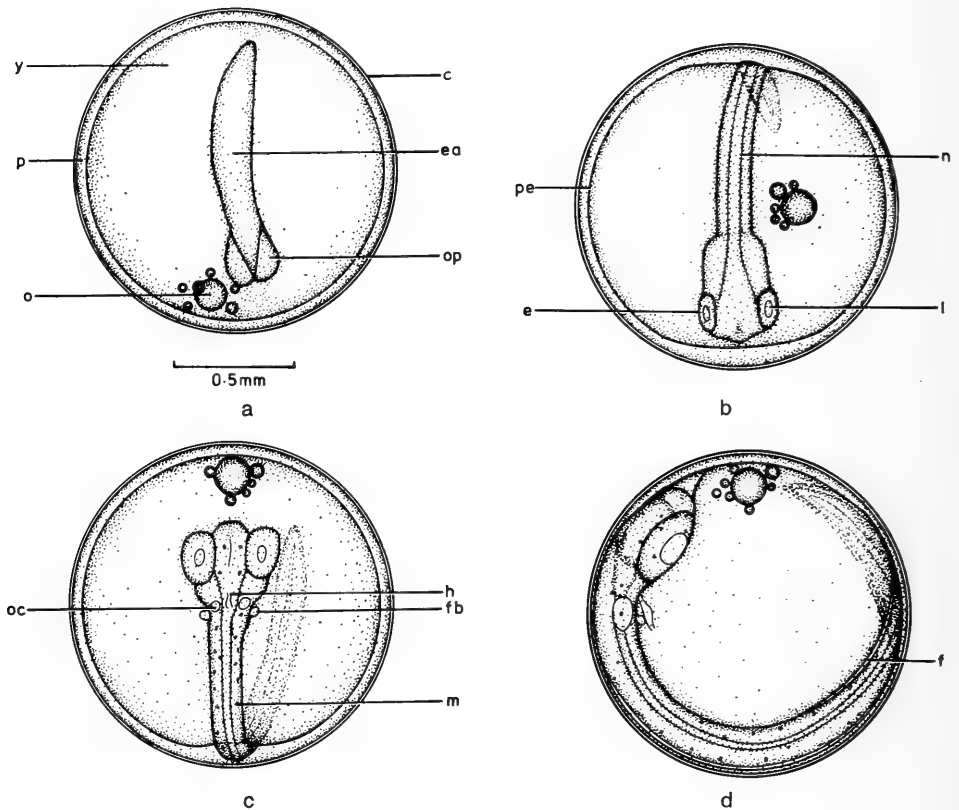


FIG. 3. Eggs of *C. fluviatilis* (adhesive filamentous strands not shown).

- (a) When collected (approximately 17 hours after fertilisation). c, chorion; ea, early embryo; o, oil globules; op, optic capsule; p, perivitelline space; y, yolk.
- (b) 17 hours after collection (approximately 34 hours after fertilisation). e, eye; l, lens; n, neurochord; pe, extraembryonic periblast.
- (c) 25 hours after collection (approximately 42 hours after fertilisation). fb, fin buds; h, heart; m, melanophores; oc, otic capsule.
- (d) 32 hours after collection (approximately 49 hours after fertilisation). f, fin fold.

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Spawning was induced only when temperatures throughout the water column were above 23.6°C and there was some water flow.

EMBRYONIC DEVELOPMENT

Eggs from infertile recently stripped ova were demersal, spherical and rather opaque at first (Figure 2b) because they possessed an irregular covering of adhesive filamentous strands. These ova became more transparent later. (Mean diameter of ova when stripped 1.29 (0.86-1.52) mm, 30 minutes later 1.46 (1.37-1.53) mm). Oil globules in these eggs were numerous and dispersed throughout the yolk and the chorion was relatively thick. The heavy telolecithal yolk of the egg no doubt gave rise to meroblastic or discoidal cleavage. The 2 fertilised eggs collected from the pond had already undergone some development when found. Assuming that the rates of development of these eggs are similar to those of other species of fish, it would appear that these two eggs were first photographed at approximately 17 hours after fertilisation. When collected, the eggs (diameter 1.32 mm and 1.34 mm) possessed five and eleven oil globules respectively (diameter 0.04-0.15 mm) grouped in clusters at the vegetal pole of the eggs. The perivitelline space was very small (width <0.03 mm). The young embryo could just be recognised at this time (length 1.08 mm, body width 0.16 mm) (Figure 3a). The optic vesicles were also visible (0.22 x 0.09 mm) (head width 0.22 mm).

By 17 hours after collection (approximately 34 hours after fertilisation) (Figure 3b) the developing larva was nearly half way around the yolk, the neural tube was apparent and the eyes were well formed (length 0.15 mm) and possessed a lens or pupil (diameter 0.07 mm) (head width 0.33 mm). At 25 hours after collection (approximately 42 hours after fertilisation) (Figure 3c) the otic capsules first appeared (diameter 0.04 mm). The fin buds were also apparent at this time and melanophores appeared on the head and body. The eyes continued to increase in size and the heart which beat at 121 beats per minute was first noticed. The body now reached 2/3rds of the way around the yolk. At 32 hours after collection (approximately 49 hours after fertilisation) (Figure 3d) the larva reached 4/5ths of the way around the yolk. The fin fold, particularly in the posterior half of the body, could be recognised easily and the numbers of melanophores present increased slightly. No noticeable decrease in volume of the yolk was observed at this stage. (Dimensions: eyes 0.33 x 0.16 mm, pupils 0.14 x 0.07 mm, otic capsules 0.14 x 0.08 mm, length of pectoral fin buds 0.05 mm, width of body 0.16 mm). At 56 hours after collection (approximately 73 hours after fertilisation) (Figure 4a) pigmentation was just commencing to be laid down in the eyes, the number of melanophores along the body increased and they also first appeared on the extra-embryonic periblast covering the yolk. The body now encircled the yolk once and the yolk was noticeably less in volume leaving a wider perivitelline space. The larva moved its tail freely at this time. The swim bladder was also now recognisable (length 0.16 mm) alongside which another organ, the liver, now appeared (length

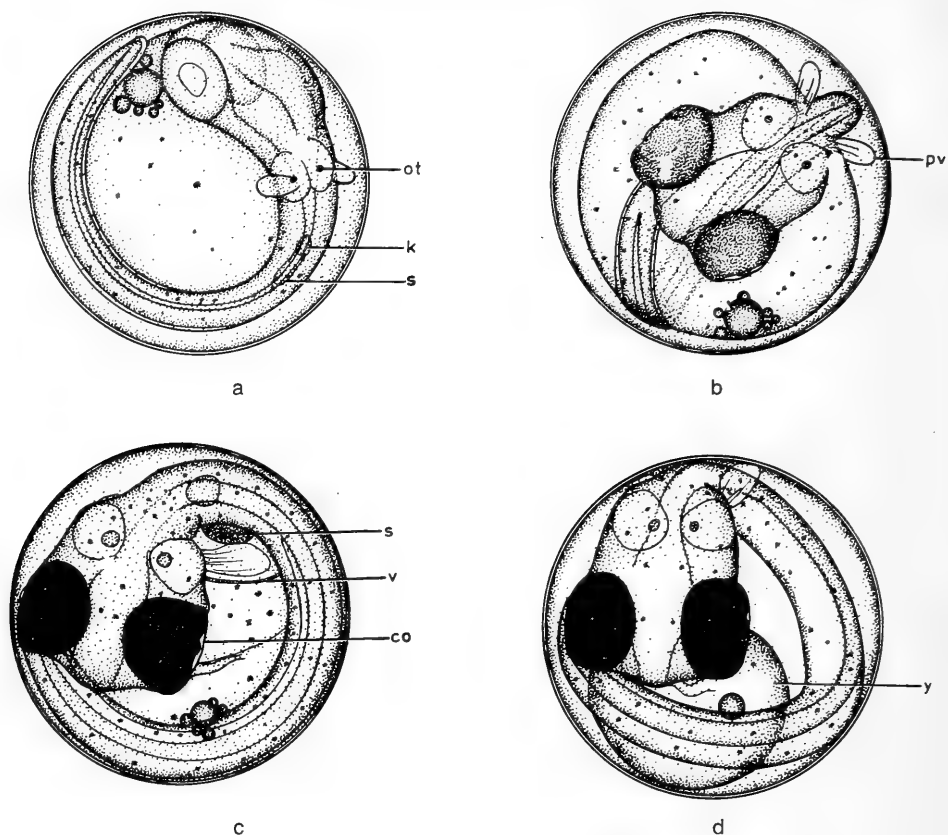


FIG. 4. Eggs of *C. fluviatilis* (adhesive filamentous strands not shown).

- (a) 56 hours after collection (approximately 73 hours after fertilisation). ot, otolith; k, liver; s, swim bladder.
- (b) 75 hours after collection (approximately 92 hours after fertilisation). pv, pectoral fins.
- (c) 102 hours after collection (approximately 119 hours after fertilisation). s, swim bladder; v, vitelline blood vessel; co, cornea.
- (d) 121 hours after collection (approximately 136 hours after fertilisation). y, yolk.

0.08 mm). By 75 hours after collection (approx. 92 hours after fertilisation) (Figure 4b) the eyes were completely pigmented black and the lenses could be seen within them; considerably more melanophores were present around the yolk, and red pigment in the blood in the heart was obvious for the first time. The body at this stage was more than once around the yolk, which had shrunk further in size (1.18 x 1.04 mm). The head had enlarged considerably by this time (width 0.69 mm) (otic capsules depth 0.24 mm, length of pectoral fin 0.21 mm). At

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102 hours after collection (approx. 119 hours after fertilisation) (Figure 2c and 4c) the liver turned red in colour (width 0.12 mm) and the swim bladder (length 0.20 mm) had a reticulate appearance (possibly large cells). At this stage melanophores were numerous just posterior to the otic capsules, the vitelline artery was apparent, and the division of the heart into two chambers could be seen (length of heart 0.19 mm, width of heart 0.13 mm). (Dimensions: yolk diameter 0.91 mm, head width 0.74 mm, eye length 0.37 mm, pupil diameter 0.15 mm, otic capsule width 0.22 mm, otolith diameter 0.06 mm). By 121 hours after collection (approx. 138 hours after fertilisation) (Figure 4d) the yolk sac had diminished to 0.74 mm in diameter leaving a large perivitelline space, and movement of the prolarva caused some flexing of the chorion. The oil globules had coalesced into a single oil globule pale yellow in colour (diameter 0.10 mm) and the larva coiled about 1 1/4 times within the egg. The body was 0.22 mm in depth behind the yolk sac and the fin fold and neural tube were quite distinct. Both eggs died shortly after this so no further development was observed, but it appears that larvae would be at least 3.4 mm in length at hatching. The temperature of water in petri dishes fluctuated between 23.3°C and 27.8°C during ova development.

THE ADULTS

Throughout most of the year and particularly outside the breeding season when the fish were not in breeding colour, the sexes are difficult if not impossible to separate. The largest fish collected in the Narrandera area was 104 mm in length. They are silvery white in colour merging to a yellow or greenish colour dorsally. The abdominal area is markedly silver (Figure 2a). There is a silvery median lateral band which becomes less marked anteriorly as it approaches the operculum. The large scales in the dorsal region are edged by small black specks. The ventral edge of the body, between the anterior edge of the anal fin and the base of the caudal fin, is pigmented black. The eye is large, the mouth small and the posterior end of the maxilla does not reach the anterior edge of the eye. This species can be separated readily from two other inland species which are superficially similar, namely *Retropinna semoni* and *Galaxias planiceps*, by the two large dorsal fins of approximately equal size.

As the breeding season approaches the sexes can be differentiated. The males are golden in colour ventrally. No black pigment is visible around or through the membranes around the vent, and its lips, which are white in colour, are not tumid (Figure 5b). There was a slight indication of a narrower fork in the caudal fin of males. Mature males were found at 42.0 mm (total length) and 40.0 mm (caudal fork length) when they weighed 0.7560 g (Table 3). In females, by contrast, the abdominal area is silvery white and black pigment is apparent on or around the tumid lips of the vent or showing through the membranes around the vent, from the black mesovarium within (Figure 5a). The urino-genital papilla

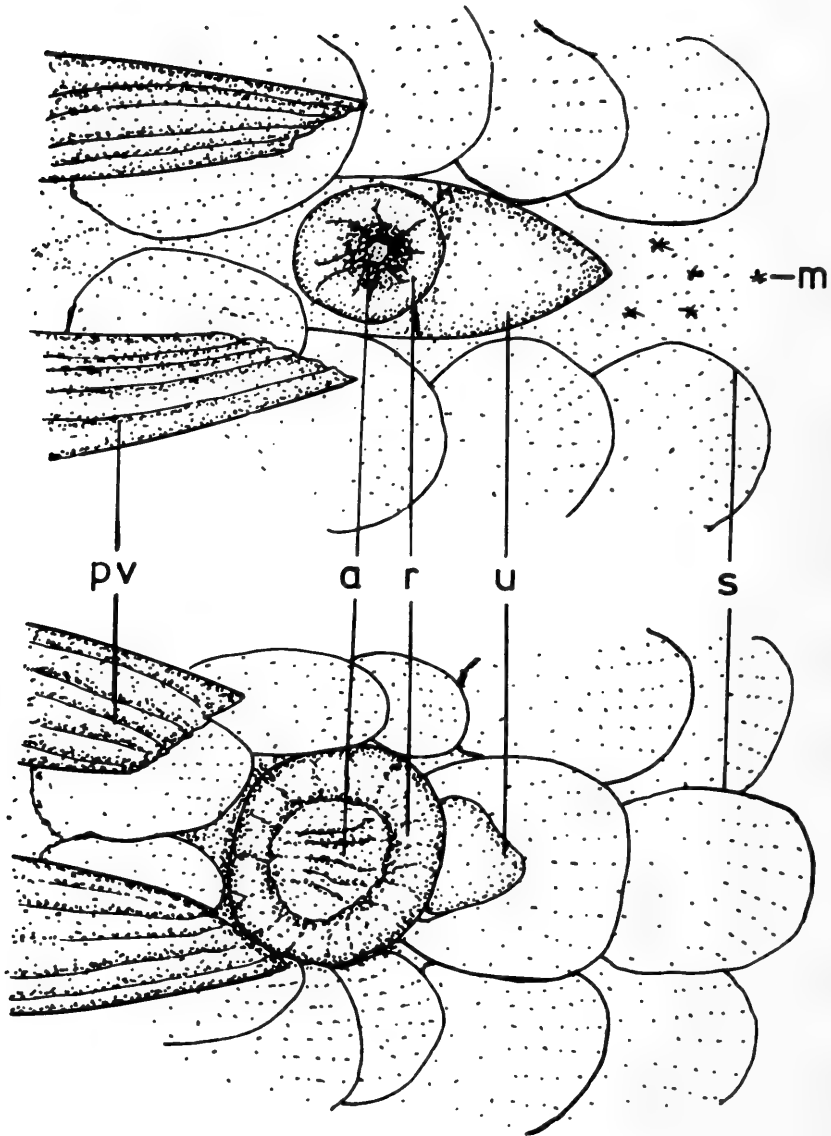


FIG. 5. (a) Above:— The vent of the female during the breeding season.

(b) Below:— The vent of the male during the breeding season. a, genital aperture; pv, pelvic fin; r, lips; u, urino-genital papilla; s, scales; m, melanophores.

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is transparent and flattened dorso-ventrally. The fork in the caudal fin appeared to be slightly wider than in males.

Mature females were found at 47.1 mm (total length) and 45.4 mm (caudal fork length) when they weighed 0.9805 g (Table 2). Although the rate of growth (Figure 6) has not been measured for fish smaller than 21.0 mm total length, growth estimates suggest that the males and females could mature at 1 year old in favourable conditions.

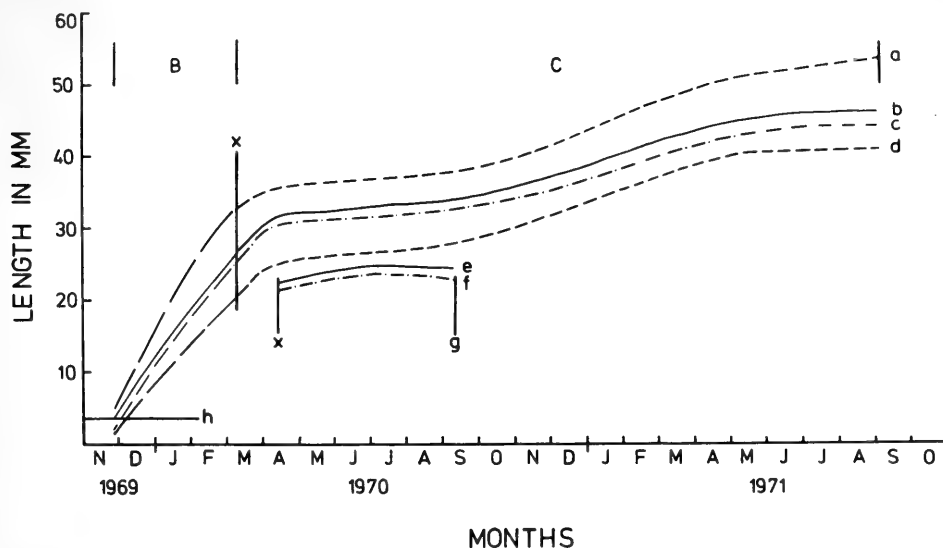


FIG. 6. Graph showing relationship between the length of fish and age for two groups of six kept in an aquarium (C). The estimated growth of one of the groups prior to capture is also shown (B). a, total length of largest fish initially collected from pond; b, average total length of group of fish initially collected from pond; c, average caudal fork length of group of fish initially collected from pond; d, total length of smallest fish initially collected from pond; e, average total length of group of six fish collected from Roach's Regulator; f, average caudal fork length of group of six fish collected from Roach's Regulator; g, all fish of this group died; h, length of larvae at hatching (approximately 3.4 mm); x, date at which fish were placed in aquaria.

FECUNDITY

Ovaries and testes were not sampled on a regular basis due to lack of sufficient material, but the material available is summarised below.

The ovaries of *Craterocephalus* spp. are covered in a black mesovarium, are single and their length attains approximately 16% of the total length of the fish. The lining of the abdominal cavity is also black. Since there appears to be a progressive development of ova in the ovary during the spawning period which

appears to last well in excess of one month for any particular fish, the ova were divided therefore into three size ranges for counting purposes (i.e. 0.04-0.10, 0.11-0.90 and above 0.90 mm). Ova in the smallest grouping are transparent, possess little if any yolk and are too small and numerous to count. Ova in the medium grouping possess some yolk and are less transparent. The large ova possess large amounts of yolk, making them almost opaque, and also possess numerous oil globules, most of which were distributed peripherally.

Ovary conditions suggest that the breeding season extended from mid October to mid February. During this season ova were found in the ovaries up to 1.52 mm in diameter (Table 2). It seems likely that ova have to be at least 1.30 mm in diameter before spawning commences since attempts to strip fish and fertilise their ova when ova were less than 1.33 mm in diameter were unsuccessful. From mid February to late September no large-sized ova were found in the ovary; the largest eggs found during this period (Table 2) were 0.46 mm from a fish apparently not spawned by 18 February and 0.40 mm from a fish approaching the spawning season on 25 August. The maximum G.S.I. (Gonosomatic index = $(\text{wt. of gonad} \times 100) / \text{wt. of body}$; Belsare 1962) for this period was 4.4. This period is no doubt outside the spawning season since no large ova were found in the ovaries examined.

It therefore appears that ripening of ova is a continuing process during the breeding season and the medium size ova continually develop into the larger ova while spasmodic spawning is taking place. The mean G.S.I. values for each month from August to the following March inclusive were 2.8, 4.4, 11.9, -, 3.1, 8.7, 5.9, 1.0 respectively. Towards the middle of February no more large ova develop, although the G.S.I. may still be as high as 6.2; this gradually drops to a level as low as 0.4 when the ovaries are quiescent. By the end of February the ovaries become noticeably vascular and were presumably resorbing (Lake 1967; Mackay 1973). The highest G.S.I. recorded for a female *C. fluviatilis* was 13.1 and the number of large and medium sized ova present in the ovaries varied from 20-107 and 459-2200 respectively (Table 2), for fish ranging in size from 0.78 to 3.28 g in weight and 47.1 to 78.5 mm in total length. There appeared to be no correlation between number of ova present in the ovary and size of fish in the samples examined.

The G.S.I. and ova counts of *C. fluviatilis* were lower than those measured in four individual females of the species *C. eyresii*. *C. eyresii* had G.S.I.'s ranging from 14.2-17.4 and ova counts of 73-144 ova above 0.90 mm in diameter and 1132-1701 ova between 0.11 and 0.90 mm in diameter in their ovaries (Table 2). Their largest ova were also slightly larger in diameter than those found in *C. fluviatilis*. The dates of collection for the three female *C. eyresii* from Inverell are not known.

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The testis of *C. fluviatilis* is white to cream and single lobed. It has a number of clefts running longitudinally along it, with the largest cleft along the mid ventral line. The lining of the abdominal cavity of males possesses only a few melanophores dorsally, in contrast with that of females.

Outside the breeding season males were recorded with G.S.I.'s as low as 1.2 and in the breeding season the G.S.I. was as high as 7.2 for fish varying in size from 0.70 to 2.88 g in weight and 42.0 to 75.0 mm in total length. Milt could sometimes be obtained from males with a G.S.I. in excess of 4.7 (Table 3). The mean G.S.I. values for October, January, February and March were 7, 4.1, 3.4 and 1.8 respectively. The single male *C. eyresii*, and one *C. fluviatilis*, had parasitised testes; the former had a G.S.I. of 12.7 and was heavily parasitised by a digenean which caused the inflated G.S.I. value. The season during which males were ripe followed closely the pattern shown by females.

GROWTH AND LENGTH FREQUENCY

Rarely are large numbers of Hardyheads taken in inland New South Wales. However, the samples taken at Lake Talbot (Figure 7 & Table 1) 26 days apart seem to indicate rapid growth during March judging by the length frequency differences. It is to be assumed that these fish are all 0+ years of age and that the sample is random.

The growth rates of 6 fish collected from a pond at the Inland Fisheries Research Station, Narrandera in early March, and kept in an aquarium are shown in Figure 6 (a, b, c and d). Growth was slow between April and August and more rapid during the summer months as was to be expected. The net growth of captive fish appears to be far slower than wild fish (Figure 6) as would be expected from their poor condition and lack of breeding in aquaria. Larvae are approximately 3.4 mm in length at hatching, and when measurements of growth were commenced the mean total length of the young fish was 26.2 mm. Using the growth rate of wild fish in Lake Talbot (Figure 7) as an index, it would appear that these were progeny from the early summer (November-December) prior to the commencement of the experiments. Examination of scales to determine the age of fish did not clarify the position. A further sample of six fish obtained from Roach's Regulator treated in a similar way died after 5 months (Figure 6e and f).

DISTRIBUTION

Collections on hand (Table 1) indicate that *C. fluviatilis* is present in the Murray, Murrumbidgee, Lachlan and Darling River Systems although data is very patchy for much of the State. Ivantsoff and Glover (1974) record *C. eyresii* from the Namoi, Peel and Murray Rivers and the inland lakes of Victoria and South Australia; added to this is the record at Elsmore near Inverell on the Macintyre

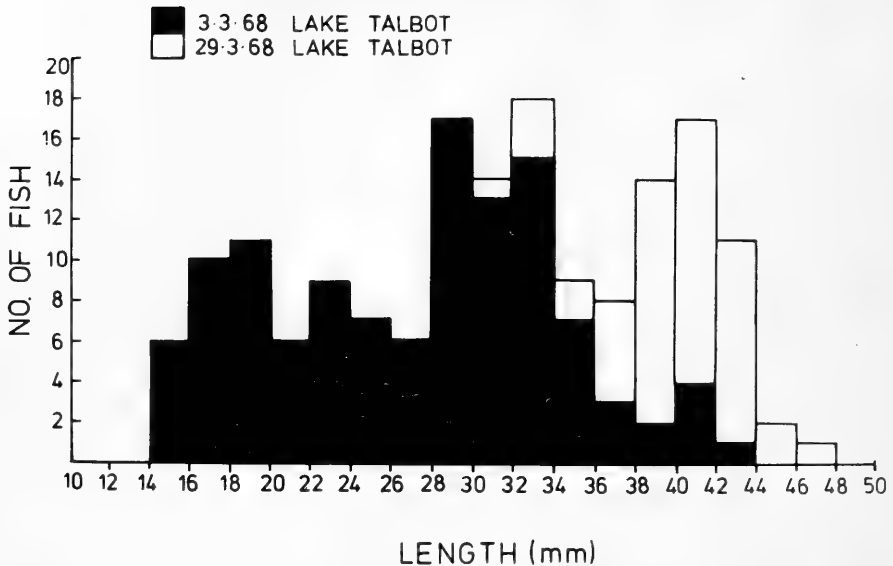


FIG. 7. Length frequency of fish collected at lake Talbot (3 March 1968 $n = 117$, 29 March 1968 $n = 49$).

River. The occurrence of *C. eyresii* throughout the inland of New South Wales has no doubt been overlooked prior to the work of the above authors and the two species of *Craterocephalus* may well be sympatric throughout their range.

DISCUSSION

The major characters differentiating the egg of this species from eggs of other freshwater species of fishes from inland New South Wales are its diameter (i.e. approximately 1.33 mm), the cluster of small oil globules, the heavily pigmented eyes of the larvae at the time of hatching, the covering of adhesive strands on the outside of the egg, and its small perivitelline space. Only two other species of inland fish described to date have similar-sized eggs. These are, *Nannoperca australis australis*, the Southern Pigmy Perch, the eggs of which have an average size of 1.28 mm (Llewellyn 1974), and *Galaxias planiceps*, the Flat Headed Minnow, which has eggs varying between 1.3 and 1.6 mm in diameter (Llewellyn 1971). In both of these species, the eggs have a larger perivitelline space and do not have a covering of adhesive threads as in *C. fluviatilis*.

The adhesive filaments on the eggs of *C. fluviatilis* are like many of the Atherinidae (Silversides) (Breder and Rosen 1966). These filaments serve as organs of attachment to submerged objects. In this character, the eggs of this

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species are similar to those of *Melanotaenia fluviatilis*, a closely related species occurring in inland New South Wales. However the adhesive filaments on the eggs of *M. fluviatilis* are clustered in a group at one point unlike those shown in figure 2b.

This type of egg would be advantaged if spawning took place in weedy areas which offered attachment for them. Since adults are found often in such a locality, it is likely that eggs are laid in these areas.

The considerable variation in ova diameter in the ovary during the breeding season suggests an extended breeding season, since withdrawal of eggs from the egg-stock for undergoing maturation would have to be a continuous process for a prolonged period (Hickling and Rutenberg 1936). Parental care of eggs is not likely to be carried out by this species, because of the prolonged spawning season brought about by the progressive development of ova within the ovary, and the presence of adhesive threads on the ova. Indeed, Breder and Rosen (1966) stated that "among the oviparous forms of the Order Mulgiliformes, in which the demersal eggs are equipped with adhesive threads, parental care is rarely present". The extended spawning period and presumably the random dispersal of eggs throughout weedy areas would play an important factor in the survival of this species which has a relatively low fecundity.

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Early Stages of Tail Regeneration in *Lampropholis guichenoti* (*Lacertilia: Scincidae*)

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ABSTRACT

Tail regeneration in the scincid *Lampropholis guichenoti* (Dumeril & Bibron) was studied using histological techniques. This study suggests that tail regeneration in this species follows the same overall pattern as has been described for several species overseas.

INTRODUCTION

Reptiles are the highest vertebrates to possess any significant powers of regeneration. They are however considerably less well endowed in this respect than the Amphibia and their capacity extends only to a few organs such as the tail and, in the case of chelonians, the carapace. The regenerated appendages are never perfect replicas of the original.

The power of regeneration of the tail is found in many lizards including members of the Gekkonidae, Pygopodidae, Scincidae, Agamidae and Anguidae (Hardy and Hardy, 1977). The ability to regenerate damaged tails is also found in some Crocodilians (Bellairs, 1969), and in the Tuatara from New Zealand.

In lizards, the ability to grow a new tail is usually associated with a facility for shedding the old one by autotomy through predetermined planes of weakness (Bellairs, 1969).

Substantial work has been done on lizard tail regeneration overseas (Hughes & New, 1962; Simpson, 1964; Bryant & Bellairs, 1967; Cox, 1969). However, in spite of this, to the author's knowledge little work in this field has been attempted in Australia. Hardy & Hardy (1977) described tail regeneration in the agamid *Physignathus lesuerii* but not from a histological standpoint. This study is concerned with some histological features of tail regeneration in the small scincid *Lampropholis guichenoti*.

MATERIAL AND METHODS

Twelve original-tailed *L. guichenoti* (Dumeril & Bibron) were collected around the Macquarie University campus at Marsfield, N.S.W. A lizard with an original tail was identified as one without any change in colour or scale pattern along the length of the tail. The snout-vent lengths of all lizards varied between 35 and 45 mm. The lizards were housed in a glass aquarium measuring 60 cm x 30 cm x 35 cm. This was fitted with a gauze lid and was not provided with artificial heating. For the duration of the study the temperature within the aquarium ranged between 15 and 26°C. The lizards were fed on a diet which consisted mostly of moths of the family Phycitidae. *L. guichenoti* does reasonably well in captivity and the condition of the animals was maintained.

Autotomy was induced by a sudden twisting of the tail and occurred in all cases between 15 and 20 mm from the vent. All tails were initially removed on the same day. After set periods (0, 2, 6, 11, 19 & 30 days), a further 5 to 14 mm section, depending on the length of the regenerated portion (the regenerate) was removed from two lizards each time. These lizards were then discarded.

The material was fixed in Bouin's fixative for 48 hours, followed by decalcification using formic acid, dehydration, and infiltration with paraffin wax at 58°C. The material was then embedded in paraffin wax and sections cut at 10 and 15 microns. The sections were stained using the Mallory-Heidenhain rapid one step method (Humason, 1972).

RESULTS

Immediately after autotomy (Fig. 1) the spinal cord, the remaining portion of the most posterior vertebra and the fat bands protude substantially further out from the stump than the muscle segments. This is the normal pattern seen in autotomized tails in skinks giving rise to a serrated appearance due to separation of the muscle along connective tissue septa.

Two days after autotomy (Fig. 2) the soft tissues of the stump are covered by a scab through which the remaining portion of the autotomized vertebra projects. Within the neural canal the spinal cord has withdrawn a short distance.

KEY TO FIGURES

ac—apical cap; bl—blastema; bv—blood vessels; c—developing cartilaginous tube; ca—caudal artery; can—canal of spinal cord; ct—cartilaginous tube; cv—caudal vein; dm—developing muscle cells; ds—developing scales; ep—epidermis; epp—epidermal papilla; es—region of endymal sac; et—endymal tube; f—fat band; fp—fracture plane through vertebral centrum; gcb—groups of nerve cell bodies; ivc—inter-vertebral cartilage; m—segmented muscle bands of tail; ms—connective tissue septa; mrs—mature regenerated scales; n—longitudinal nerve; nf—newly differentiated fat band; pv—remaining portion of most posterior vertebra; rm—regenerated muscle; s—space between new and old muscle; sc—scab; spc—spinal cord; ver—vertebra; xspc—site of breakage of spinal cord.

TAIL REGENERATION IN A SCINCID LIZARD

PLATE I

Fig. 1. Horizontal section through tail immediately after autotomy.

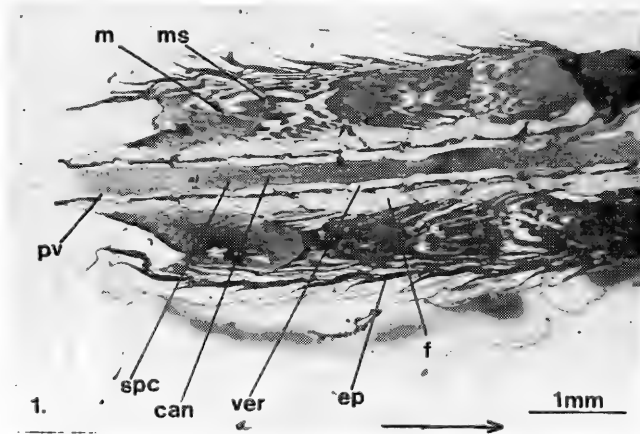


Fig. 2. Parasagittal section through tail two days after autotomy.

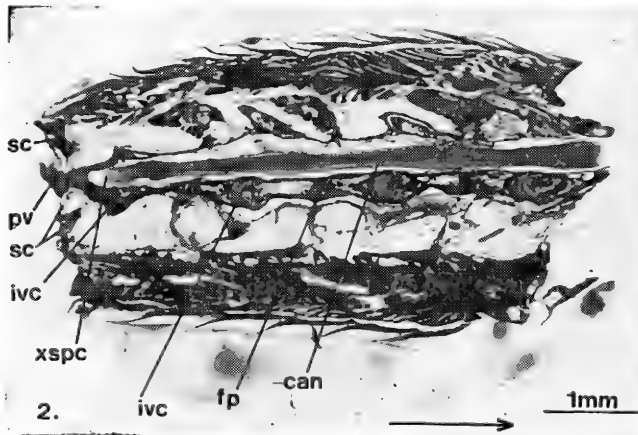
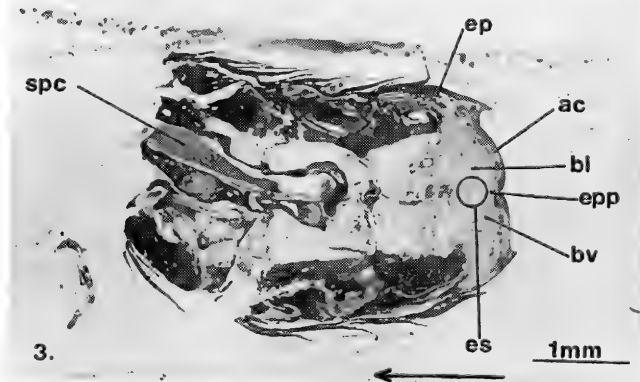


Fig. 3. Parasagittal section through tail six days after autotomy.



Arrow indicates the anterior direction.

PLATE II

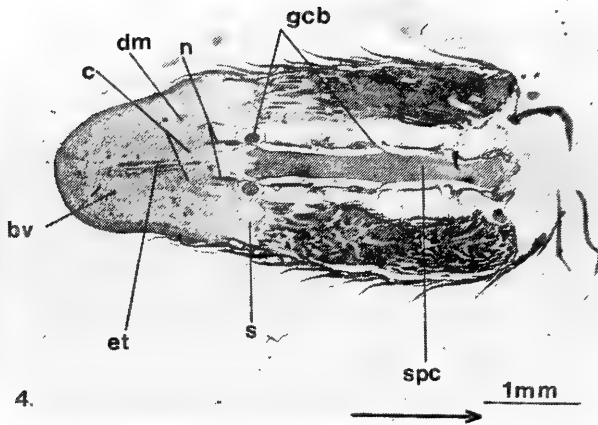


Fig. 4. Horizontal section through tail eleven days after autotomy.

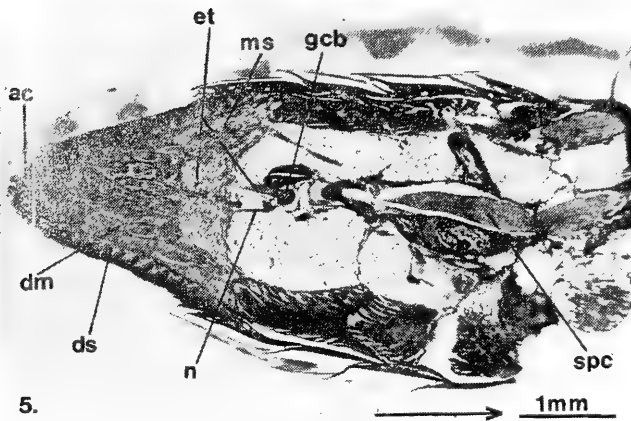


Fig. 5. Parasagittal section through tail nineteen days after autotomy.

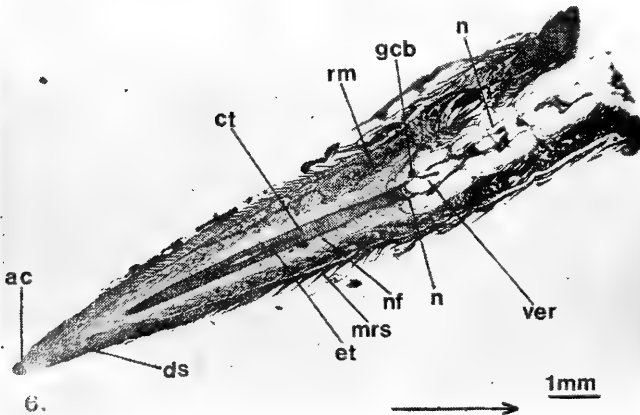


Fig. 6. Oblique horizontal section through tail thirty days after autotomy.

Arrow indicates the anterior direction.

TAIL REGENERATION IN A SCINCID LIZARD

After six days (Fig. 3) the scab has disappeared and the blastema is readily apparent. The blastema consists of undifferentiated cells from which nearly all the tissues of the new tail will be formed (Bellairs, 1969). The blastema is a bowl-shaped structure, the peripheral edge of which approaches the original tail musculature. The wound is covered by new epidermis which forms a smooth covering known as the apical cap. At the centre of the apical cap is an indentation called the epidermal papilla. This indicates the presence of the ependymal sac and hence the ependymal tube (Hugh & New, 1962), although neither of these structures is actually visible in Fig. 3.

By eleven days the stump is beginning to increase noticeably in length (Fig. 4). The ependymal tube is readily visible. The mesenchyme surrounding the ependymal tube is beginning to differentiate into cartilage. At this point these muscle cells closely resemble cells of smooth muscle. A wide space exists between the new developing muscle and the old muscle. Hughs & New (1962) claim that this region is occupied by loose mesenchyme which is heavily infiltrated with lymphocytes. Hughs & New (1962) also note that at this point there has differentiated a plexus of blood vessels surrounding the ependymal sac. These blood vessels are visible in Fig. 4 as small dark areas at the distal end of the regenerate. Two longitudinal branches of the spinal nerves can be seen passing alongside the developing cartilaginous tube. These nerves will in the future comprise the greater part of the regenerate's nerve supply (Bellairs, 1969).

By nineteen days (Fig. 5), the development of scales is noticeable. Also by this stage the muscle is becoming segregated into blocks separated by connective tissue septa.

By thirty days (Figs. 6 & 7), considerable further development has occurred. The cartilaginous tube surrounding the ependymal tube is well developed. The new muscle, quite well developed and segmentally arranged in the proximal portion of the regenerate, is less well developed distally. A similar situation exists for the scales. Lying ventrally in the fat band between the muscle layer and the cartilaginous tube are two major blood vessels, the caudal artery and the caudal vein (Fig. 7).

DISCUSSION

After autotomy there is a latent period before the regenerate begins to grow significantly. For *L. guichenoti* in this study it was approximately six days. This is in line with results of other workers in this field. Bellairs (1969) notes a latent period prior to the commencement of regeneration of seven to fourteen days for *Lacerta vivipara*; Bryant & Bellairs (1967), six to ten days for *Lacerta dugesii*; Hughs & New (1962), approximately ten days for the gekkonid lizard *Sphaerodactylus*. During the latent period the scab is shed and the initial blastema and apical

PLATE III



Fig. 7. Sagittal section through tail at the region of autotomy thirty days after autotomy (x55). Arrow indicates the anterior direction.

cap are formed. After this time the regenerate begins to lengthen quickly. Some workers have noted that in some lizards the broken vertebra is either resorbed or comes away with the scab (Bryant & Bellairs, 1967; Bellairs, 1969; Cox, 1969). This is not necessarily the case with *L. guichenoti* for although the autotomized vertebra is not visible in the specimens depicted in Figures 2 and 3, it is clearly visible in Fig. 7 and has not appeared to impede regeneration.

Shortly after the end of the latent period, (approx. six days) the ependymal tube becomes noticable as an outgrowth from the broken end of the spinal cord. It is derived mainly from the ependymal epithelium which lines the cavities of the central nervous system (Bellairs, 1969). Its tip becomes closed off to form a small sac (the ependymal sac). The tissues around the ependymal sac begin to revert to a condition resembling embryonic mesenchyme (the blastema) (Bellairs, 1969).

TAIL REGENERATION IN A SCINCID LIZARD

Hughs & New (1962) noted that within the wall of the ependymal sac, mitotic figures are more common than at any other site. Furthermore, they noted that the whole appearance of the ependymal sac suggests that it is the active centre of cellular proliferation and is the main site of new cell production for the whole region of regeneration. The importance of the ependymal tube is stressed by Simpson (1964), who noted that it is the ependymal lining of the central canal which is the primary initiator of tail regeneration in the scincid lizard *Lygosoma laterale*. According to Simpson (1964), failure of a regenerate to differentiate a cartilaginous tube is associated with the absence of a regenerated ependymal lining (ependymal tube).

The spinal cord of the uninjured lizard tail is analogous to the ependymal tube of a regenerated tail. Some nerve fibres occur within the ependymal tube but the greater part of the regenerate's nerve supply comes from the last two or three pairs of spinal nerves above the level of the injury (Bellairs, 1969). When the tail is shed, fibres of the severed proximal ends of these nerves regenerate and enter the wound (Figs. 4 & 5). Hughs and New (1962) note that this occurs within two days of autotomy in the gekkonid lizard *Sphaerodactylus*. As the blastema enlarges there is a corresponding elongation of each nerve. These longitudinal nerves occur in the loose mesenchyme between the cartilaginous tube and the region of the muscle bands (Hughs & New, 1962) (see Fig. 5).

The cartilaginous tube first differentiates from the mesenchyme of the blastema after approximately eleven days in *L. guichenoti*. In a mature regenerate it may become calcified, but never becomes segmented or separated into bony vertebrae.

The appearance of new developing scales is seen by nineteen days after autotomy. Fully mature scales are present on the proximal portion of the regenerate by thirty days.

SUMMARY

In the early regeneration of the tail in *L. guichenoti* several stages can be recognised.

1. Formation of a scab over the wound and the withdrawal of the spinal cord (two days).
2. Formation of new epidermis and the blastema beneath the scab followed by loss of the scab (less than six days).
3. Growth of the ependymal tube into the blastema and formation of the ependymal sac (less than six days).
4. Early differentiation of the blastema into muscle and cartilaginous tube. Appearance of blood vessels at the distal end of the blastema. Growth of longitudinal nerves into the blastema (six to eleven days).

5. Further differentiation of the blastema, including segmentation of muscle into blocks separated by connective tissue septa. Development of scales from new epidermis (less than nineteen days).

6. Appearance of mature regenerated scales at the proximal end of the regenerate. The proximal end of the regenerate is now fully differentiated into cartilaginous tube, fat band, muscle segments, scales etc. (nineteen to thirty days).

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Body Growth in some Australian Rodents

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ABSTRACT

Body growth, as measured by weight, head and body length, tail length and pes length is presented for 16 species or subspecies of Australian rodents from the time of birth to 140 or 180 days (60 days in five cases). There is no clear separation of species into fast or slow growers, but the growth curve for members of the genus *Rattus* was more complex than that of hydromyine rodents.

INTRODUCTION

Over the last eight years I have bred small numbers of many species of Australian rodents and kept records of their rate of growth. For most of these species little is known about their growth rates and as a consequence aging of captured specimens is difficult. The data is presented here in the hope that it will partially rectify this deficiency and also contribute to the comparative study of the growth rates of Australian rodents.

METHODS

The parental stocks were obtained from the following localities; *Rattus tunneyi tunneyi*, northern N.T.; *R.t. culmorum*, Woodgate and Byfield, Qld; *R. fuscipes coracius*, Atherton Tableland, Qld; *R.f. greyi*, Pearson Island, S.A.; *R. leucopus leucopus*, Iron Range, Qld; *R.l. cooktownensis*, Atherton Tableland, Qld; *R. colletti*, northern N.T.; *Pseudomys apodemoides*, south-eastern S.A.; *P. delicatulus*, Emerald and Mapoon, Qld; *P. higginsi*, Cradle Mt., Tas.; *Zyzomys woodwardi* and *Z. argurus*, northern N.T.; *Melomys cervinipes*, Home Rule, Qld; *Conilurus penicillatus*, northern N.T.

Animals were housed in small groups, in cages varying in size from 38 x 25 x 15 cm to 55 x 38 x 20 cm. *Conilurus* and *Uromys* were housed in cages 90 x 65 x 40 cm. Animals were fed a diet of mixed seed and mouse cubes supplemented twice weekly with diced apples and carrots. Water, to which a small amount of

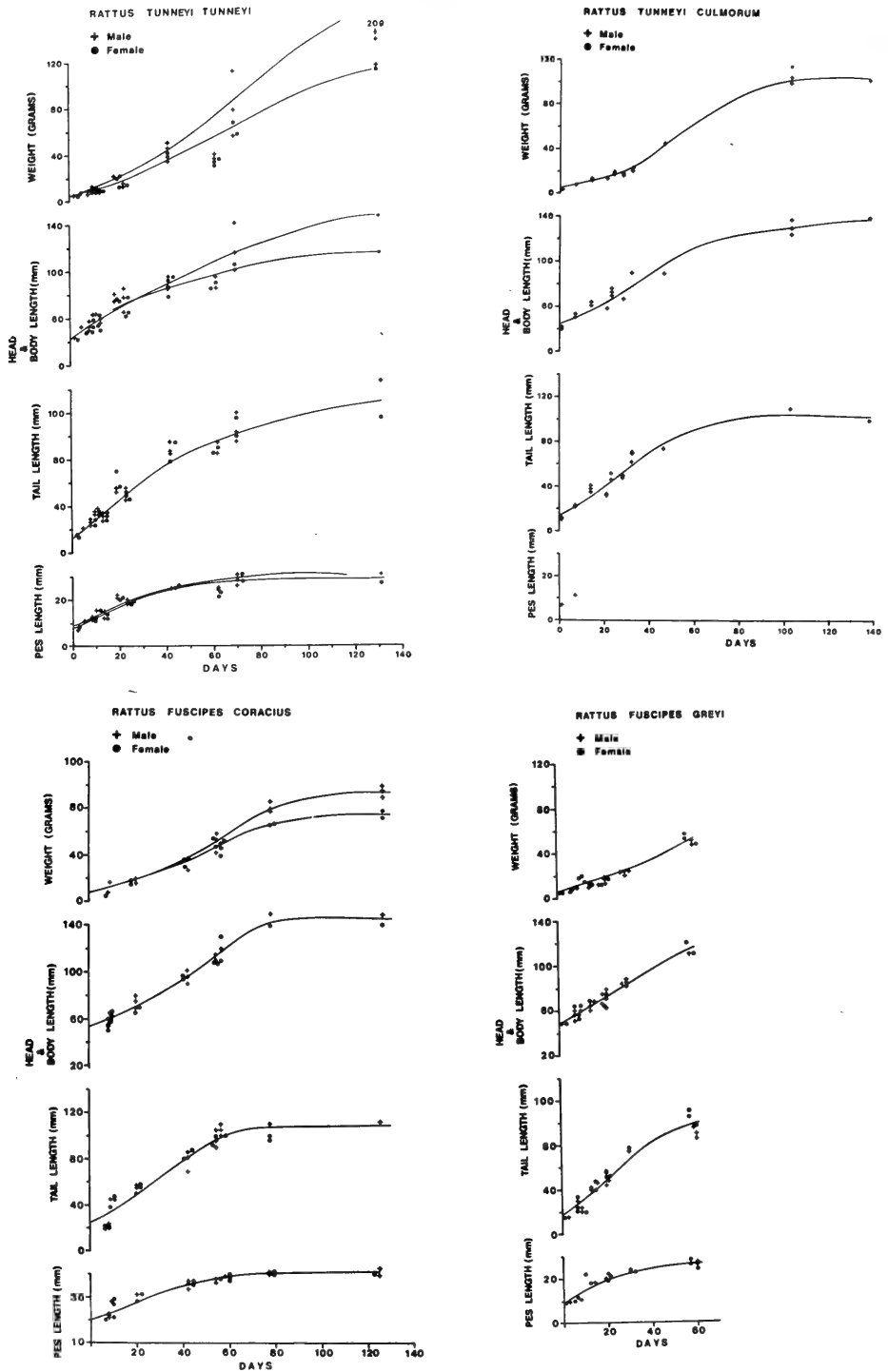


FIG. 1. Growth rates of *Rattus tunneyi tunneyi*, *R.t. culmorum*, *R. fuscipes coracius* and *R.f. greyi* as measured by changes in weight, head and body, tail, and pes length. Curves fitted by eye.

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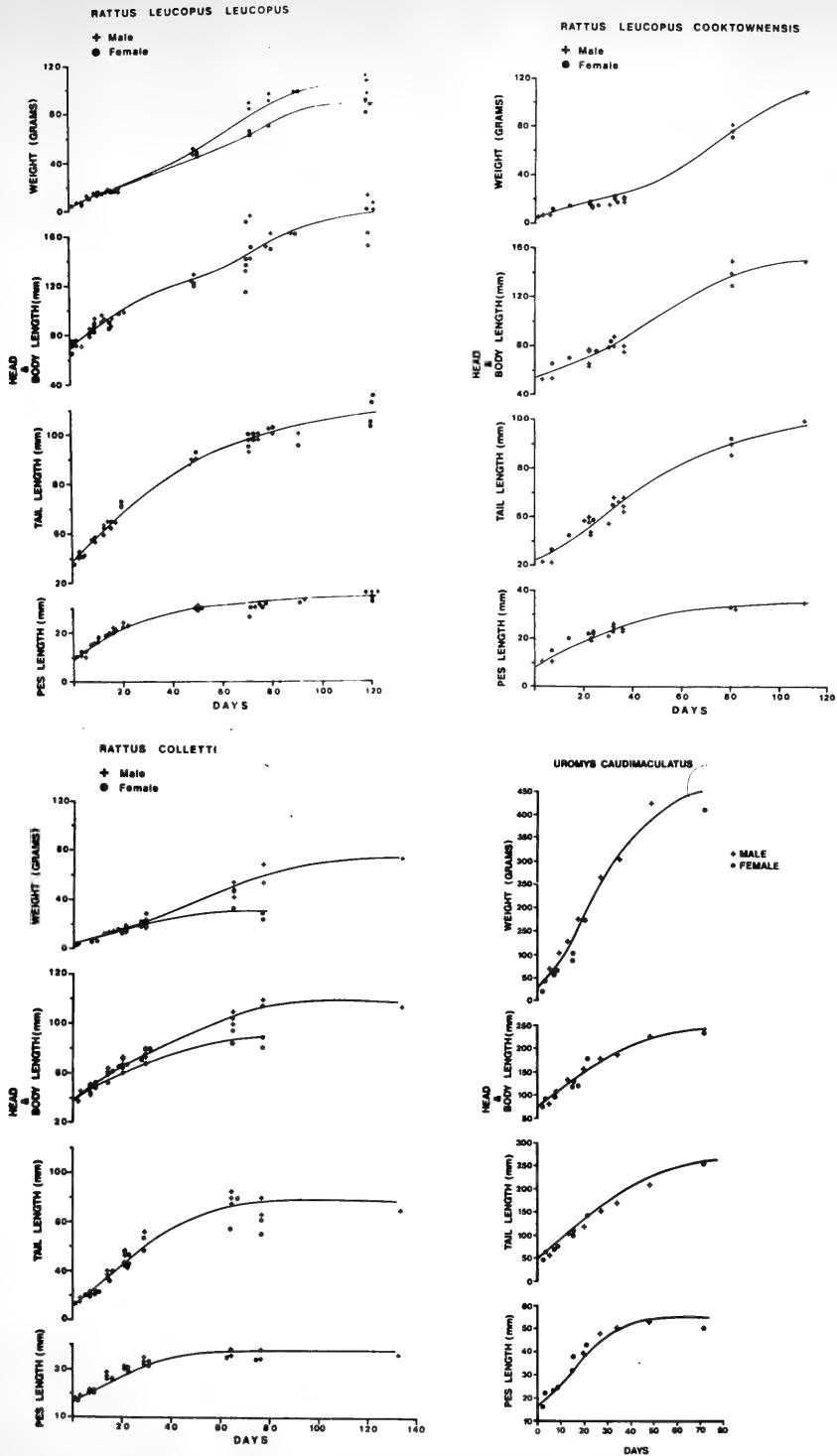


FIG. 2. Growth rates of *Rattus leucopus leucopus*, *R.l. cooktownensis*, *R. colletti* and *Uromys caudimaculatus* as measured by changes in weight, head and body, tail, and pes length. Curves fitted by eye.

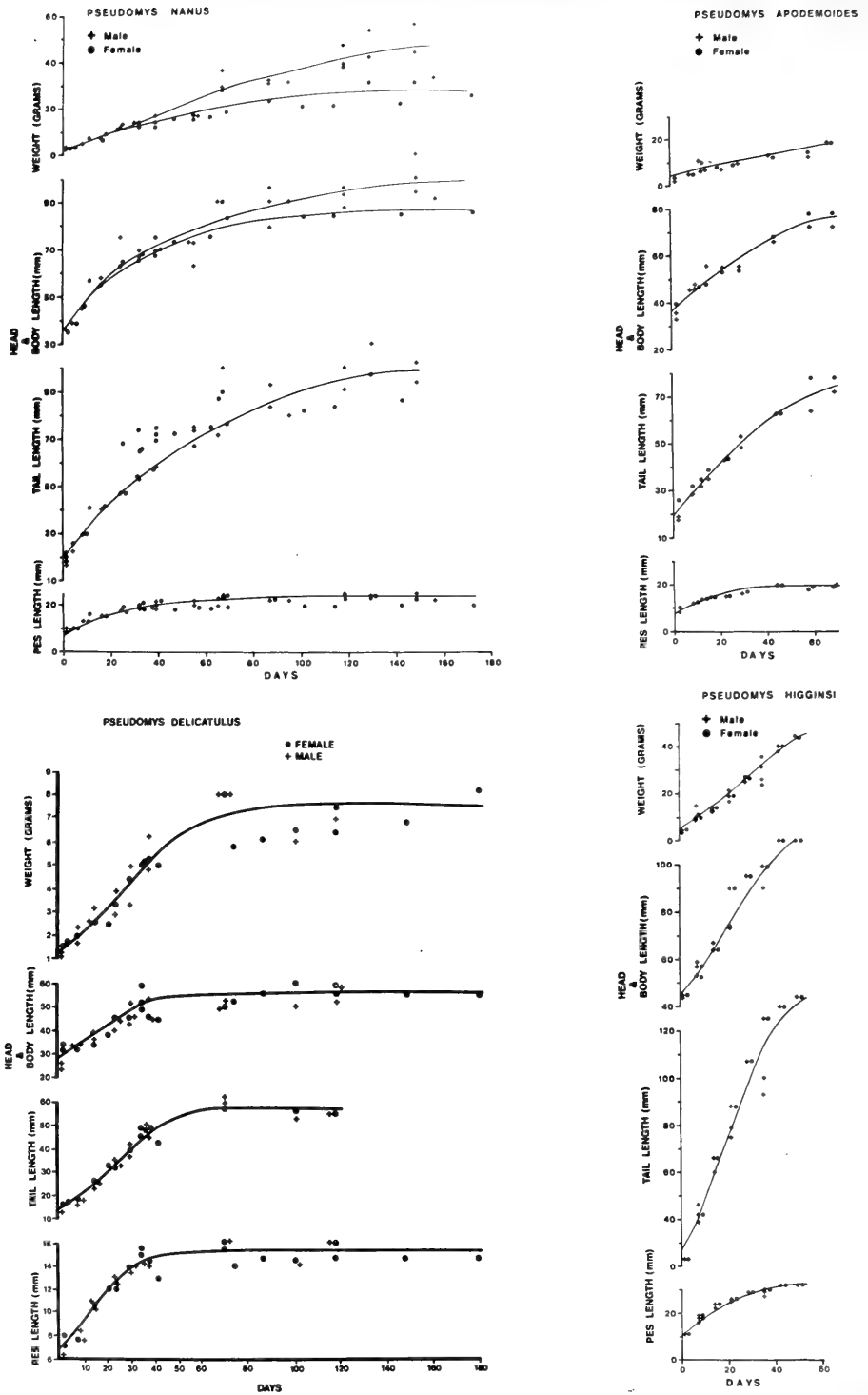


FIG. 3. Growth rates of *Pseudomys nanus*, *P. apodemoides*, *P. delicatulus* and *P. higginsii* as measured by changes in weight, head and body, tail, and pes length. Curves fitted by eye.

GROWTH IN AUSTRALIAN RODENTS

infant formula multivitamin mix (Pentavite) was added, was provided *ad libitum*. The cages were housed in air-conditioned rooms ($21 \pm 2^\circ\text{C}$) under natural lighting.

The young were weighed and their head, body, tail and pes lengths measured at approximately weekly intervals for about 60 days and thereafter at approximately monthly intervals.

Nomenclature follows Lee *et al* (in press) in the allocation of all native Australian rodents, except members of the genus *Rattus*, to the subfamily Hydromyinae.

RESULTS

Growth rates for 16 species and subspecies are shown in Figures 1-4. Interspecific comparisons between growth rates are notoriously difficult, mainly due to difficulties in defining adult weight (Morrison *et al*, 1978), but most Hydromyinae have similarly shaped growth curves and reach essentially adult weight by 100 days.

The pattern of growth of the *Rattus* species studied differed from that of the members of the Hydromyinae. In the Hydromyinae, the growth followed a smooth curve, whereas in *Rattus* growth was relatively slow for the first month of life and rapid for the next month or two. This prepubertal spurt in growth was most noticeable in the males.

DISCUSSION

In a study of the growth of *P. novaehollandiae*, Kemper (1976) used the time taken to grow from 20 to 90% of adult weight as an index of growth. Using this index with nine Australian murids she considered that they could be divided into fast and slow growers. My data does not show any evidence for separation into fast and slow growers. For example, the Kemper method applied to my data gave an index of 50 for *R. tunneyi*, but Kemper, using data from McDougall (1946), gives an index of 310. This discrepancy must stem from the difficulties in determining adult weight, especially in overfed captive animals. Thus Kemper considered year-old *R. tunneyi* or *R. sordidus* as not yet adult, whereas I consider them adult around 100 days. Most *Rattus* are reproductively mature for laboratory breeding at around 80-100 days and many individuals have stopped reproducing by 14 months. This general problem of adequately defining adult weight and also the difficulties of comparing the growth rates of different species is well covered by Morrison *et al*, (1978).

The more complex growth curves for some *Rattus* species may be associated with increased reproductive rate. Not only is the growth curve more complex, but the individual variation in size between adult *Rattus* is much more pronounced

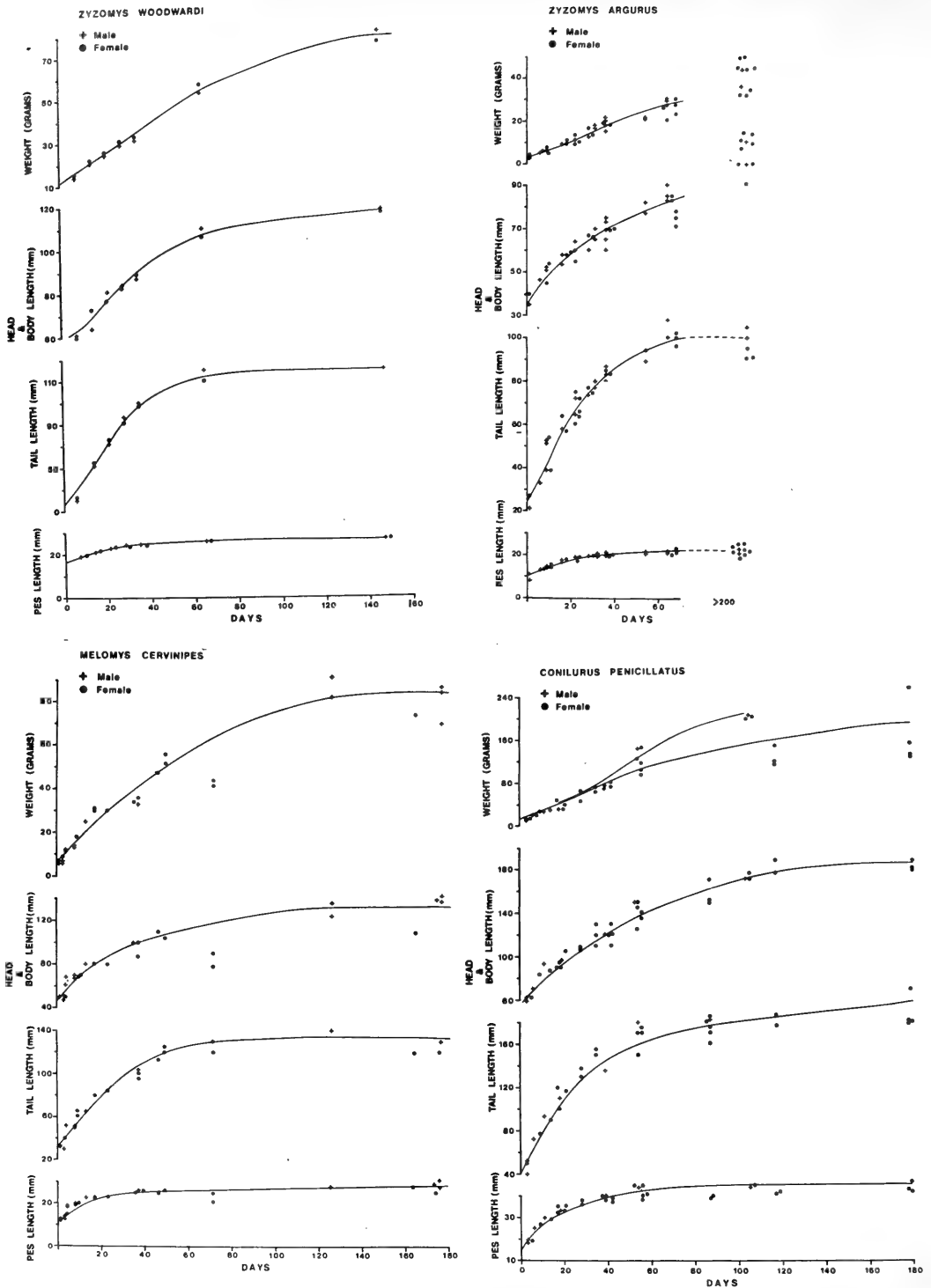


FIG. 4. Growth rates of *Zyzomys woodwardi*, *Z. argurus*, *Melomys cervinipes* and *Conilurus penicillatus* as measured by changes in weight, head and body, tail, and pes length. Curves fitted by eye. (The *Z. argurus* figure includes values for adults, i.e. 200 days old).

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than in any Hydromyinae. This is particularly true of *R. sordidus*, *R. colletti* and *R. villosissimus* (Taylor and Horner, 1973). The reason for this more complex pattern of growth is not clear at this stage, but it could be a mechanism that would allow an individual to slow its growth and start breeding or to continue to grow and defer breeding to a more advantageous time, depending on prevailing environmental conditions.

The rarity (at least in captivity) of many of these species and the resulting small sample sizes make detailed comparison between the growth rates of the different species unwarranted. However, it is hoped that the results will be of use as an aid to the aging of specimens of the different species, either in conjunction with ecological studies or in the study of museum specimens.

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Reproductive Parameters of some Australian Rodents

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ABSTRACT

Data are given for oestrous cycle length, gestation length and litter size of the following Australian rodents: *Leggadina forresti*, *L. lakedownensis*, *Pseudomys delicatulus*, *P. hermannsburgensis*, *P. shortridgei*, *P. higginsi*, *P. albocinereus*, *P. apodemoides*, *P. nanus*, *Conilurus penicillatus*, *Zyomys argurus*, *Z. woodwardi*, *Notomys fuscus*, and *Uromys caudimaculatus*.

Most species of Hydromyinae had an oestrous cycle of 6-10 days, a gestation period of 30-40 days and litter size of 2-4 young. *Z. woodwardi* with an 18 day oestrous cycle and *P. nanus* with a 23 day gestation are exceptions.

Members of the Hydromyinae do not appear to have been under selection pressure to increase their fecundity. This is in contrast to members of the genus *Rattus* which have been under selection pressure to increase their reproductive rate and may have reached a point where it is physiologically difficult to shorten rate and may have reached a point where it is physiologically difficult to shorten their oestrous cycle length and gestation period, although their average litter size could possibly be increased.

INTRODUCTION

The reproductive potential of a species is an important aspect of that species' adaptation to its environment and hence has a direct bearing on its ecology and conservation. In this study the reproductive parameters of oestrous cycle length, gestation length and litter size are investigated for some little-known species of native rodents.

METHOD

The species used, where they were collected and the number of individuals used are given in Table 1.

Females were housed individually, or with a male, in cages varying in size from 38 x 25 x 15 cm to 55 x 38 x 20 cm. The *Conilurus* and *Uromys* were housed in cages 90 x 65 x 40 cm. Animals were fed a diet of mixed seed and

TABLE 1

Oestrous cycle lengths and litter sizes for some Hydromyinae rodents.

Species and collecting locality	Oestrous cycle length (days)		Litter Size	
	Mode	Data	Mode	Data
<i>Leggadina forresti</i> Northern S.A.	8	a) 8,8,8,8,8,8,8,7 b) 7,7,7,7,7,7,8,7	3	4,3,3
<i>L. lakedownensis</i> Lakeland Downs, Qld.	7	a) 7	3	3
<i>Pseudomys delicatulus</i> North Qld.	6	a) 6,6,6,6	3	3,2,1,4,3,3,3,2,3, 3,3,1,3,3,2,1
<i>P. hermannsburgensis</i> Northern S.A.	8	a*) 8,13,7,12 c*) 8,9 b*) 9,8,8 d*) 7	3	3,3,6,4,3,3,2,3,3, 3
<i>P. shortridgei</i> Portland, Vic.	10	a) 11,10,10		
<i>P. higginsii</i> Cradle Mtn., Tas.	16	a) 16 b) 12,13,16,19,15	4	4,2,3,4,2,2,4
<i>P. albocinereus</i> Jurien Bay, W.A.	7	a) 7,7,7,8,10,9,10,8,9,8,7,7,7 6,8,6,6,6,7,7,7, b) 10,9,10,10 c) 7,8,7,7 d) 9	4	4,4
<i>P. apodemoides</i> South East, S.A.	—		2	3,4,2,2,3,3,4,4,2, 5,2,2
<i>P. nanus</i> N.W. W.A. & North N.T.	6	a) 5,7,6,6,7 b) 6,7,6,5 c) 6,5,5,5,5,6 d) 6,6	3	3,3,2,3,5,1,3,4,3
<i>Conilurus penicillatus</i> Arnhem Land, N.T.	9	a) 9 b) 9,9,8,10,9,9,12 c) 9,9 d) 9	2	3,3,1,1,2,2
<i>Zyzomys argurus</i> Arnhem Land, N.T.	7	a) 7,7,7,7,7,7,7,7,7,7,6,6,6,6, 7,7,7,6,7,7,7, b) 7,7,7,7,7,7 c) 7,5,7,7,7,6,7 d) 6,7,6,7,7,7,6	4	5,4,3,3,4
<i>Z. woodwardi</i> Arnhem Land, N.T.	18	a) 18,18,18,16 b) 18,18 c) 18	2	2
<i>Notomys fuscus</i> Betoota, Qld.	7	a) 7,7,7,7,7,6,7,8 b) 7,8,7,8,8,8,8,7,8 c) 7,7,7, 7,7,8 d) 8,7,7,7,6,8,7,9,8,9	3	2,4,1,3,4,5,4,3,3, 3,2,3,2,3,3,3,1,3, 5,4,3
<i>Uromys caudimaculatus</i> Cape York, Qld.	7	a) 7,7,7,7,7,7, b) 7,6,7,7 c) 7,7,7,7,7,	1	1,3,1,1,2

a-d = Different individuals. **Indicate male present.**

* = Animals caught near Curtin Springs, N.T. and maintained at Medical School Animal House, University of Adelaide. Data collected by W. G. Breed.

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mouse cubes supplemented twice weekly with diced apples and carrots. Water, to which a small amount of infant formula multivitamin mix (Pentavite) was added, was provided *ad libitum*. The cages were housed in air-conditioned rooms ($21 \pm 2^\circ\text{C}$) under natural lighting. Animals were checked daily except Saturday. Vaginal smears were taken six days a week with the aid of a wire loop. Smears were placed on slides, air dried, stained with 1% methylene blue, and the relative proportions of cornified and nucleated epithelial cells and leucocytes recorded with the aid of a binocular microscope. Oestrous cycle lengths were scored from the peak of one cornification to the day before the next peak of cornification. In situations where the lack of a smear on Saturday produced an ambiguous result, the result has not been used. Gestation periods were ascertained by the interval between the recording of sperm in the vaginal smear to the day of parturition or, in some cases, by the interval between consecutive litters.

Nomenclature follows Lee *et al* (1980) in the allocation of all native Australian rodents, except members of the genus *Rattus*, to the subfamily Hydromyinae.

RESULTS

Table 1 gives the length of time between consecutive cornified smears (oestrous cycle lengths) and litter sizes for fourteen species of Hydromyinae. The minimum figure for the former is likely to be the oestrous cycle length.

For many of the species, cycle lengths are available for females housed either separately or with a male. The results (Table 1) showed that the presence of a male made no difference to the length of the oestrous cycle.

All but three species had oestrous cycles of between six and nine days; *Zyzomys woodwardi* had a cycle length of 16-18 days, *Pseudomys higginsii* one of 12-19 days with a mode of 16, and the one female *P. shortridgei* had a cycle length of 10-11 days.

Average litter sizes were also generally between three and four. Only in *Uromys caudimaculatus* and *Conilurus penicillatus* was there good evidence that litters averaged less than three.

Gestation lengths generally ranged from 30-40 days with the notable exception of *P. nanus* which had a considerably shorter gestation with a mode of 23 days (Table 2).

DISCUSSION

Many of the species discussed here are rare (at least in captivity) and for some, only one or two females were available for study. Thus sample sizes are small and the data collected will require confirmation.

The figures given in Table 1 and 2 suggest a pattern for reproduction within the Hydromyinae of an oestrous cycle of 6-10 days, a gestation period of 30-40 days, and a litter size of 2-4. *Z. woodwardi* and *P. bigginsi* with an oestrous cycle of 18 days and 16 days respectively, and *P. nanus* with a gestation of 23 days are exceptions. This pattern contrasts with that of Australian *Rattus* species which have an oestrous cycle of 4-5 days, a gestation period of 20-22 days and litter sizes of 4-7 (Breed, 1978). Fig. 1 graphically illustrates these differences using data from this study, and from Taylor and Horner (1973a), Breed (1978) and Lee et al (1980).

Each of the parameters plotted in Fig. 1 can be analysed on the assumption that it is physiologically impossible for an individual to increase its rate of reproduction beyond certain limits.

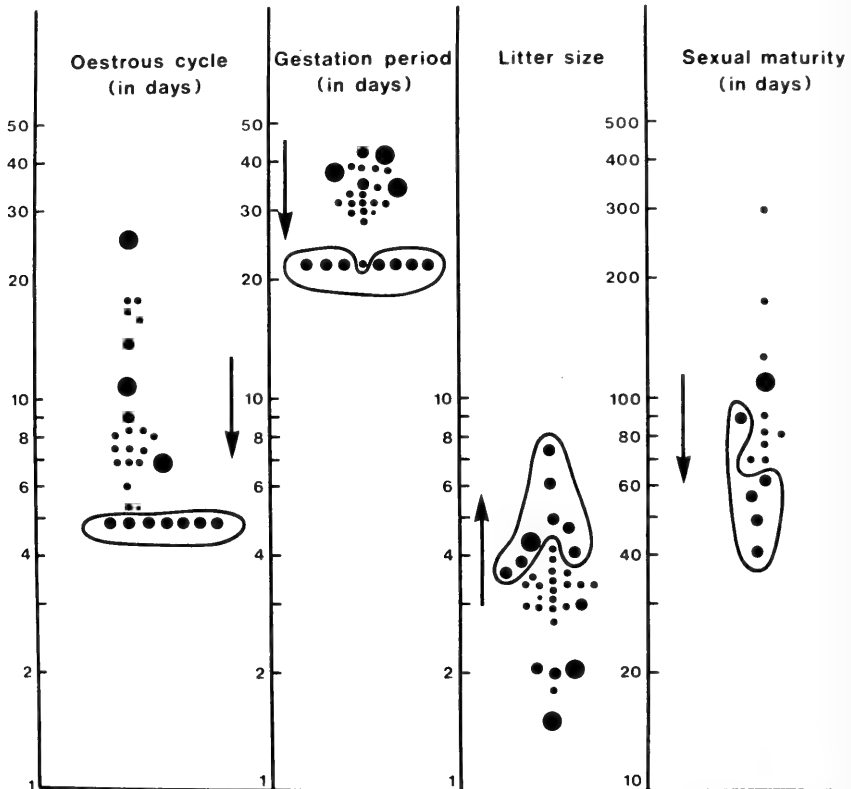


FIG. 1. Chart of oestrous cycle lengths, gestation lengths, litter sizes and age at sexual maturity for some Australian rodents. Values for species of *Rattus* circled. Arrow indicates direction of increased fecundity. Data is derived from this paper, Breed (1978): Lee et al (1979) and Taylor and Horner (1973a). Size of spots roughly proportional to size of species.

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There is good evidence that an oestrous cycle of less than about four days is physiologically impossible (Hoffman, 1973). Thus, the reason all seven *Rattus* species have the same oestrous cycle lasting about four days may simply be that it is the shortest possible. To achieve a more rapid reproductive rate, oestrous cycling would have to be replaced by induced ovulation as has happened in some rodents (e.g. *Microtus*).

Similarly, Fig. 1 suggests that 22 days may be the shortest gestation period possible for a rodent, but the golden hamster (*Mesocricetus auratus*) is known to have a 15-18 day gestation period (U.F.A.W., 1972). This is exceptional and it may be that although gestation periods shorter than 20-22 days are possible they are difficult to achieve. The clustering of the gestation periods of the Hydromyinae between 30 and 40 days indicates that this is an optimum length for these species. Why this is so is unknown.

With respect to litter size, there is no evidence that any Australian rodent has reached a physiological limit, if indeed there is one. Several species of *Rattus* (e.g. *R. norvegicus*) have considerably larger litters than does any Australian rodent. The clustering of average litter sizes of the Hydromyinae between three and four indicates that this is an optimum litter size for these species. All species

TABLE 2 Gestation lengths, in days, of some Hydromyinae rodents

Species	Gestation length		Data from which gestation length derived	
	Range	Mode	Sperm to parturition	Intervals between litters
<i>Leggadina lakedownensis</i>	33	—	33	—
<i>Pseudomys delicatulus</i>	31-37	31	—	31,31,35,37,31,34, 35
<i>P. higginsii</i>	32,31*	—	32	—
<i>P. albocinereus</i>	38	—	38	—
<i>P. apodemoides</i>	35	—	—	35
<i>P. nanus</i>	22-27	23	23,23,24,23	22,24,22,22,23,23, 23,27,22,27,23,22, 23,23,23,25,24,24, 25
<i>P. hermannsburgensis</i>	30-34	33	—	34,30,33,33
<i>Conilurus penicillatus</i>	36	—	36	—
<i>Zyzomys argurus</i>	32-34	—	34	32
<i>Notomys fuscus</i>	33-38	33	33,36,33,38, 35,34	—
<i>Uromys caudimaculatus</i>	41	—	41	—

* = From pairing to parturition.

of Hydromyinae have only four nipples to which the young of most species cling tenaciously for long periods. This combination of structure and behaviour effectively prevents litters of more than four surviving intact. Thus to increase the litter size, ovulation rate and either nipple number or suckling behaviour would both have to change simultaneously. In some species (e.g. *Notomys alexis* and *Hydromys chrysogaster*) this has apparently happened and litters of up to eight young can be successfully reared. Nevertheless there does seem to be a partial barrier to Hydromyinae increasing their litter sizes. This situation does not occur in *Rattus*.

Age at sexual maturity varies greatly between species and there is no evidence of any limit or barrier having been reached although there does seem to be a clustering of values around 50 to 90 days.

The above data suggest, albeit in a rather general way, that there are limits to the values of each of these parameters, and possibly also that there may be partial barriers at certain points. Species of *Rattus* seem to have reached these limits for both oestrous length and gestation period, and some may be approaching the limit for age at sexual maturity.

In contrast, the Hydromyinae do not appear to have reached the limit for any of the parameters except possibly for gestation period in the case of *P. nanus*. They may, however, have reached a partial barrier with litter sizes due to a combination of structural and behavioural factors.

Thus it appears that members of the genus *Rattus* have been under selection pressure to increase their reproductive rate and can now probably only do so readily by increasing their litter size. In contrast members of the Hydromyinae show little evidence of having been under selection pressure to increase their reproductive rate. Should these pressures change, reproductive rates could be increased by varying any or all the four parameters discussed. Two species of Hydromyinae may be doing this *N. alexis* by increasing its litter size and decreasing its age at sexual maturity, and *P. nanus* by decreasing its gestation period.

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A Report on a Collection of Mammals from Southwest Papua, 1972-1973

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ABSTRACT

A survey of the mammals in southwest Papua New Guinea was made in 1972-73 and thirty-nine indigenous and four introduced species are discussed. The indigenous species consist of one monotreme, 14 marsupials, 8 rodents, and 16 bats. The introduced species include the feral dog, feral pig, house rat and rusa deer. Five species are new records for Papua New Guinea and an additional three are new range extensions into southwest Papua.

INTRODUCTION

The southwest corner of Papua New Guinea is part of the Trans-Fly Plains, and is extremely interesting in terms of mammalian taxonomy. It appears to be the area of overlap between the Australian and the New Guinea-Indonesian mammalian fauna. Schodde and Calaby (1972) actually consider the fauna of this area to be an outlier of the northern Australian fauna, only recently separated in geological time by the Torres Strait. Some of the species reported, especially among the bats, appear to have characteristics midway between previously described species from Australia and others from West Irian-Indonesia, suggesting the existence of clines instead of separate species or subspecies. The fauna in this area is relatively undisturbed as the human population is low, being only about one person per three square kilometres.

ENVIRONMENT

A) Topography, Geology and Soils

The area covered by this survey is roughly 8000 square kilometres, bounded on the west by the West Irian-Papua New Guinea border up to Weam in the northern corner, eastward across to Dimisisi and Southward down to the coast

(see Fig. 1). The land is low and slightly undulating, with a maximum elevation of 55 metres above sea level along the Morehead Ridge. This ridge runs roughly east-west extending from Korombo to halfway between Mata and Derideri.

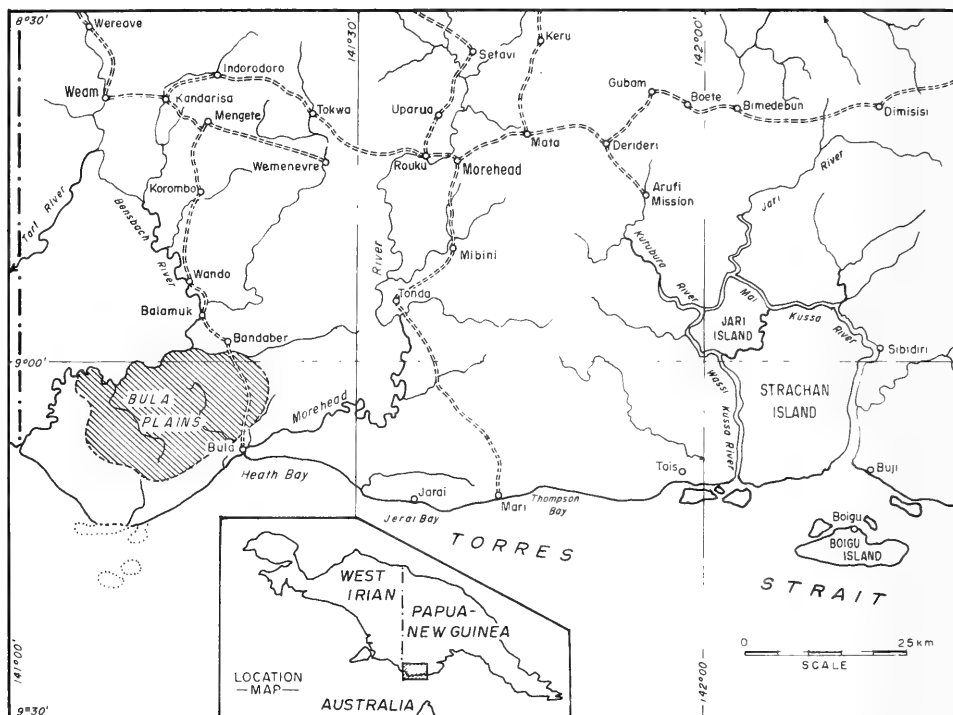


FIG. 1. Map of area surveyed showing places mentioned in the text.

Geologically the area consists of the Oriomo Plateau and a coastal plain. The plateau is made up of Pleistocene clay, and is broken by the broad and low Morehead Ridge. The coastal plain is divided into a back plain of recent clay, and a coastal strip of flats, low beach ridges and swales of recent littoral clay and sand.

B) Climate

The survey area has a monsoonal climate. Using ten years data from Morehead, the average annual rainfall is 1682 mm, with about 77% falling in the wet season between December and May. At the height of the wet season only the Morehead and other smaller ridges are above water, whereas at the end of the dry season water is present only in the larger rivers and billabongs.

REPORT ON A COLLECTION OF MAMMALS

TABLE 1

SYSTEMATIC LIST OF THE MAMMALS IN SOUTHWEST PAPUA

MONOTREMATA

Tachyglossidae

- 1) Short-beaked echidna

Tachyglossus aculeatus lawesi

MARSUPIALIA

Dasyuridae

- 2) Red-cheeked marsupial mouse
3) Marsupial mouse
4) Papuan marsupial mouse
5) Marsupial cat

Sminthopsis rufigenis
Sminthopsis new form
Planigale novaeguineae
Dasyurus geoffroi

Peramelidae

- 6) Spiny bandicoot
7) Rufescent bandicoot
8) Brindled bandicoot

Echymipera kalubu oriomo
Echymipera rufescens rufescens
Isoodon macrourus moresbyensis

Phalangeridae

- 9) Spotted phalanger
10) Long-fingered possum
11) Common striped possum
12) Sugar glider

Phalanger maculatus goldiei
Dactylonax palpator
Dactylopsila trivirgata kataui
Petaurus breviceps flavidus

Macropodidae

- 13) Agile wallaby
14) Red-legged wallaby
15) Dusky wallaby

Macropus agilis papuanus
Thylogale stigmatica oriomo
Thylogale bruijni bruijni

CHIROPTERA

Pteropodidae

- 16) Big-eared flying fox
17) Central flying fox
18) Bismarck flying fox
19) Collared flying fox
20) Greater naked-backed bat
21) Long-tongued fruit bat
22) Common blossom bat
23) Southern blossom bat
24) Common tube-nosed bat
25) Pallas' tube-nosed bat

Pteropus macrotis epularius
Pteropus alecto gouldii
Pteropus neohibernicus papuanus
Pteropus scapulatus
Dobsonia moluccensis magna
Macroglossus lagochilus nanus
Syconycteris crassa papuana
Syconycteris australis
Nyctimene albiventer
Nyctimene cephalotes

Emballonuridae

- 26) Bare-rumped tomb bat
27) Intermediate tomb bat

Taphozous nudicluniatus
Taphozous mixtus

Molossidae

- 28) Wrinkle-lipped mastiff bat
29) Beccari's mastiff bat

Tadarida jobensis
Tadarida beccarii

Vespertilionidae

- 30) Lesser New Guinea pipistrelle
31) Sanborn's evening bat

Pipistrellus tenuis
Nycticeius sanborni

RODENTIA

Muridae

- 32) Common water rat
33) Native-mouse
34) Little melomys
35) Rufescent melomys
36) Mottle-tailed tree rat
37) House rat
38) Dusky field rat
39) Southern spiny rat
40) Brush-tailed rabbit rat

Hydromys chrysogaster beccarii
Pseudomys delicatula
Melomys lutillus muscalis
Melomys rufescens niviventer
Uromys caudimaculatus aruensis
Rattus rattus
Rattus sordidus
Rattus leucopus
Conilurus penicillatus randi

CARNIVORA

Canidae

- 41) Domestic dog

Canis familiaris

ARTIODACTYLA

Suidae

- 42) Domestic pig

Sus scrofa papuensis

Cervidae

- 43) Rusa deer

Cervus timorensis

C) *Vegetation*

The area is basically covered with a tropical savannah, which is variously subdivided. The following vegetation types are taken from Paijmans *et al.* (1971). The Oriomo Plateau is mainly covered by tall mixed, low mixed and *Melaleuca* savannah and monsoon scrub. Tall mixed savannah consists of trees averaging 20 metres in height, with mainly a grass understory. Monsoon scrub has short scattered trees with an open to moderately dense scrub layer about one metre high, and a sedge ground cover. Low mixed savannah averages 15 metres in height while *Melaleuca* savannah consists of thin-stemmed *Melaleuca* trees averaging 10 metres tall, and both have a ground layer of grasses and sedges. The former two vegetation types occur on well to imperfectly drained sites while the latter two occupy sites of poor to very poor drainage.

The Morehead Ridge and other well drained areas are mainly covered with monsoon forest. The trees in this type of forest average 25 metres in height with an open to moderately dense canopy, and the scrub layer is moderately dense.

The coastal back plain is covered predominately by low grassland and swamp grassland with some *Melaleuca* swamp forest along the rivers, and is almost completely inundated during the wet season. Grassland is mainly low to mid-height grasses with abundant sedges and scattered *Pandanus* trees. Swamp grassland consists of almost pure *Pseudoraphis*, and low to mid-height sedge-grass vegetation. Both of these grassland types are mostly found on the Bula Plain, a 365 square kilometre area which occupies much of the coastal back plain from Bula to the Bensbach River.

The coastal strip vegetation consists of a dense littoral forest, averaging 30 metres in height, with an open understory. This forest grades into a mangrove woodland along the shore. The littoral forest is located on the nontidal flats and inland beach ridges, whereas the mangrove belt grows on the tidal flat.

D) *Land Use*

There are only about 2500 people, living in 28 villages, in the survey area. There is no industry, except for the very minor export of crocodile skins, and the local people subsist mainly on the products from their gardens, which is supplemented by hunting and fishing.

METHODS

The present survey was begun in November 1972 and was completed by December 1973. Seven collecting methods were used, some methods being more suitable for certain species than others.

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Various sizes of Elliot, Havahart, and snap traps were used. The live traps were successful for all the murids except the native mouse. These also caught native cats and Red-cheeked Marsupial Mice. Snap traps only caught Little Melomys.

No bait was particularly successful, though tinned fish and fresh crayfish caught water rats, tree rats and native cats with some degree of success. Most of the murids were trapped by putting a combination of coconut, kaukau, and a ball of peanut butter-honey-oatmeal mixture in the Elliot traps.

Mist netting was used to catch bats, and was very successful for the Megachiroptera (especially the fruit bats and blossom bats) when erected in the local village gardens. Very few Microchiroptera were caught using this method.

Galvanized iron pits, 55 cm in diameter and 90 cm deep, sunk in the ground with their tops at ground level, were very successful in catching species that could not be taken by any other method. Native mice and marsupial mice were caught in this way.

Spotlighting and shooting were the main collecting methods for flying foxes, bandicoots and cuscus. Some of the tree rats were also collected in this way.

Hunting in the daytime was used to collect species, such as the macropods, that were too large to trap.

Local people were encouraged to bring in any mammal they found. Even with substantial rewards in the form of money, tobacco, or shotgun cartridges, this method was not very successful, although most of the Microchiroptera were obtained in this way.

Elderly men from villages were questioned about rarely seen species. From the descriptions they gave, a marsupial resembling a hare-wallaby or rat-kangaroo is present in the area, but is rare and very difficult to catch.

The general references used for identification purposes were Laurie and Hill (1954) and Lidicker and Zeigler (1968). In addition to these the following references were also used:— Menzies (1973) and Tate (1951) for murids; Anderson (1912), Troughton (1925), Hill (1961), McKean (1972) and Koopman (1973) for bats; Tate (1948a) for the macropodids; Tate (1948b) for the paramelids; Tate (1945) for the phalangerids and Tate (1947) for the dasyurids.

All the specimens collected and field number cards are deposited in the collection of the Department of Agriculture, Stock and Fisheries Wildlife Section Museum in Port Moresby, Papua New Guinea. Only field numbers are given for the specimens, since only part of the collection has been converted to museum numbers. The localities listed refer to the villages nearest the collection site.

RESULTS

Systematic Account

Order MONOTREMATA

Family Tachyglossidae

Tachyglossus aculeatus lawesi (Ramsay)

Short-beaked echidna

Specimen:— Skin and skull: 0064, unsexed juv., Tais.

Notes: This species was only found along the coastal strip, where it appeared to be locally abundant and was used by the natives for food.

Order MARSUPIALIA

Family Dasyuridae

Sminthopsis rufigenis Thomas

Red-cheeked marsupial mouse

Specimen:— Skins and skulls: 0019 ♀, Morehead; 0046 ♂, Wando; 0166 ♂, Bula.
In spirit: 0336 ♂, Bimedeibun.

Sminthopsis new form

Specimens:—Skins and skulls: 0250 ♀, 0254 ♂, 0256 ♂, 0276 ♂, 0289 ♂,
0291 ♀, 0300 ♂, Morehead. In spirit: 0315 ♂, 0316 ♀, 0317 ♂,
0318 ♂, 0319 ♂, 0324 juv. ♂, 0327 juv. ♂, Morehead;
0311 ♂, 0314 ♀, 0328 juv. ♀, Mibini.

Notes: This marsupial mouse was only collected in the tall mixed savannah, using pit traps. One of the females (0250) caught in July 1973 had eight hairless young in the pouch while another (0316) caught in October 1973 had five hairless young.

Planigale novaeguineae Tate & Archbold

Papuan marsupial mouse

Specimens:— Skins and skulls: 0225 juv. ♂, Wando; 0271 ♂, Morehead.
In spirit: 0326 ♂, Morehead.

Notes: These are the first records of this species from western Papua.

Dasyurus geoffroii Gould

Specimens:—Skins and skulls: 0076 ♂, 0117 juv. ♂, Morehead; 0181 ♀,
Mibini. Skull only: 0246 ♀, Mari. In spirit: 0340 ♂, Morehead.

Note: This Dasyurid was previously unrecorded for Papua. *Dasyurus albopunctatus* Schlegel was the only native cat previously recorded in New Guinea.

Family Peramelidae

Echymipera kalubu oriomo Tate & Archbold

Spiny bandicoot

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Specimens: Skulls only: 0333-4 unsexed, Bimedebun.

Notes: The only specimens were skulls from bandicoots, which had been collected by local villagers for food.

Echymipera rufescens rufescens (Peters & Doria)

Rufescent bandicoot

Specimens:— Skin and skull: 0071 ♂, Wando. Skull only: 0032 unsexed, Bimedebun.

Notes: One specimen was shot in grassland while the other was brought in by a native.

Isodon macrourus moresbyensis (Ramsay)

Brindled bandicoot

Specimens:— Skins and skulls: 0059 unsexed, 0061 unsexed, Mari; 0069 ♂, 0070 ♀, Wando, 0118 juv. ♀, 0119 juv. ♂, Morehead, 0023 ♀, 0024 juv. ♂, Mibini. Skulls only: 0008 unsexed, 0020 ♀, 0021 unsexed, Morehead; 0108 juv. ♀, Wando; 0193 ♂, Tais.

Notes: This bandicoot was very common in most habitats. One female (0020) obtained in March 1973 had a pouched young with hair just erupting.

Family Phalangeridae

Phalanger maculatus goldiei (Ramsay)

Spotted phalanger

Specimens:—Skins and skulls: 0014 ♂, Morehead; 0204 ♀, Tais. Skulls only: 0039 unsexed, 0041-3 unsexed, 0047 unsexed, 0098 unsexed, Wando; 0114-5 unsexed, Korombo; 0187 unsexed, Tais.

Notes: This phalanger was common in wooded areas, especially near water. All of the specimens were collected by hunting, the "skulls only" specimens were taken by natives for food.

Dactylonax palpator (Milne-Edwards)

Long-fingered possum

Specimens:— none

Notes: Two live possums were obtained from local villagers before the survey started but they unfortunately escaped. They were collected while trees were being felled during road building.

Dactylopsila trivirgata kataui (Matschie)

Common striped possum

Specimens:— Skin and skull: 0030 ♂, Mibini. Skin only: 0194 ♂, Tais.

Petaurus breviceps flavidus Tate & Archbold

Sugar glider

Specimen:— Skin and skull: 0049 ♀, Dimisisi.

Notes: The sugar glider was very common in wooden areas and was often seen on blossoming banksias at night using a spotlight.

Family Macropodidae

Macropus agilis papuanus (Peters & Doria)

Agile wallaby

Specimens:— Skull only: 0006 ♂, 0127 unsexed, Tonda.

Notes: Agile wallabies were common in the grassy clearings along the rivers and on the Bula Plains. This species was the one most commonly hunted by the local villagers for food.

Thylogale stigmatica oriomo (Tate & Archbold)

Red-legged wallaby

Specimens:— Skins and skulls: 0010 ♂, 0011-2 ♀, 0245 ♂, Mibini;
0130 ♂, Tonda.

Notes: These wallabies were shot in low mixed savannah or woodland near swamps and they did not appear to be very common.

Thylogale bruijini bruijini (Schreber)

Dusky wallaby

Specimens:— Skins and skulls: 0251 ♂, 0253 ♂, Tokwa.

Notes: As opposed to the red-legged wallaby, this species was found in the thickest monsoon forest, which was an uncommon vegetation type in the survey area.

Order CHIROPTERA

Family Pteropodidae

Pteropus macrotis epularius (Ramsay)

Big-eared flying fox

Specimens:— Skins and skulls: 0125 ♂, 0126 ♀, 0131-2 ♂, Tonda; 0148 ♀,
0160 ♂, Bula; 0211 ♂, 0227 ♂, 0228-9 ♀, 0233 ♀, 0234 ♂,
0242 ♂, 0338 ♂, Wando; 0213 ♀, Morehead. Skull only:
0268 ♂, Bula.

Notes: This bat was common in the survey area and was collected mainly from low mixed savannah and the gardens of natives.

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Pteropus alecto gouldii Peters

Central flying fox

Specimens:— Skins and skulls: 0198 ♂, Tais; 0294-5 ♀, 0296 ♂, 0297 ♀, Morehead; 0339 ♀, Wando.

Notes: The central flying fox was previously unrecorded from New Guinea (McKean, 1970) but Tate (1952) states that in 1937 he collected what was apparently the identical race at Bugi, on the southern coast of New Guinea. This species is recorded from the Malay Archipelago (Laurie and Hill, 1954), from Queensland and the Torres Strait (McKean, 1970), and from the Northern Territory (Calaby and Keith, 1974). Specimens were obtained from scattered sites throughout the survey area in June and September 1973.

Pteropus neobibernicus papuanus Peters & Doria

Bismarck flying fox

Specimens:— Skins and skulls: 0145-7 ♂, Bula; 0205-6 ♂, Tais; 0298 ♂, Morehead. Skulls: 0050-2 unsexed, Dimisisi.

Pteropus scapulatus Peters

Collared flying fox

Specimens:— Skulls only: 0065, 0199-201, 0203, all unsexed, Mari.

Notes: Like the central flying fox, this Australian flying fox (Ride, 1970) was also previously unrecorded from New Guinea. It was collected by natives along the coastal strip between the Morehead and Wassi Kussa Rivers in April and June 1973.

Dobsonia moluccensis magna Thomas

Greater naked-backed bat

Specimens:— Skins and skulls: 0055-8 unsexed, Mari; 0159 ♂, 0167-8 ♂, 0174-7 ♂, Bula; 0197 ♂, Tais. Skull only: 0196 ♂, Tais.

Notes: This bat was captured only along the coastal strip. Like all of the larger flying foxes it was captured using a shotgun.

Macroglossus lagochilus nanus Matschie

Long-tongued fruit bat

Specimens:— Skins and skulls: 0123 ♀, Morehead; 0128 ♀, Tonda; 0132-4 ♀, 0262-3 ♀, Mibini; 0149 ♂, 0150 ♀, 0151-2 ♂, 0153 ♀, 0154-5 ♂, 0156-8 ♀, 0161 ♂, 0169 ♂, 0171 ♀, 0173 ♂, Bula; 0195 ♀, Tais; 0209 ♂, 0221-2 ♂, 0231 ♂, 0235-7 ♀, 0239 ♀, 0240 ♂, 0241 ♀, 0243 ♀, Wando; 0277-8 ♂, 0280 ♀, 0281 ♂, 0282 ♀, Mari.

Notes: The usual method of capture for this common species was mist netting in the gardens of local villagers although sleeping animals were sometimes captured

from the undersides of banana leaves. In June 1973 two of the captured females had enlarged teats.

Syconycteris crassa papuana (Matschie)

Common blossom bat

Specimens:— Skins and skulls: 0086 ♀, 0087 ♂, 0088 ♀, 0089-91 ♂, 0094 ♀, Morehead; 0230 ♀, 0238 ♂, 0244 ♂, Wando.

Notes: The capture techniques for this bat were the same as for the long-tongued fruit bat.

Syconycteris australis (Peters)

Southern blossom bat

Specimens:— Skin and skull: 0266 ♀, Mibini.

Notes: Only one specimen of this bat was collected using mist nets in *Melaleuca* savannah.

Nyctimene albiventer (Gray)

Common tube-nosed bat

Specimens:— Skins and skulls: 0252 ♂, Tokwa; 0265 ♀, Mibini.

Notes: One of these bats was mist netted in *Melaleuca* savannah and the other in monsoon forest.

Nyctimene cephalotes (Pallas)

Pallas' tube-nosed bat

Specimens:— Skins and skulls: 0279 ♀, Mari; 0283-5 ♀, Bula.

Notes: This species was previously recorded from the Celebes east to north-west West Irian and Ruk Island in the Admiralty Islands.

Family Emballonuridae

Taphozous nudiclunatus De Vis

Bare-rumped tomb bat

Specimen:— Skin and skull: 0288 ♂, Wando.

Taphozous mixtus (Troughton)

Intermediate tomb bat

Specimen:— Skull only: 0001 unsexed, Morehead.

Family Molossidae

Tadarida jobensis (Miller)

Wrinkle-lipped mastiff bat

Specimens:— Skins and skulls: 0134-8 ♀, 0139 ♂, 0140-1 ♀, Rouku.

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Notes: All of these specimens were collected from holes in the trunks of coconut palms by local villagers.

Tadarida beccarii (Peters)

Beccari's mastiff bat

Specimens:— Skins and skulls: 0207♀, 0208♂, 0212♂, 0214♀, 0216♀, Wando; 0261♀, Morehead.

Notes: This bat was collected from holes in *Melaleuca* trees.

Family Vespertilionidae

Pipistrellus tenuis Temminck

Lesser New Guinea pipistrelle

Specimens:— Skins and skulls: 0077-8♀, 0079♂, 0080-1 juv.♂, 0082♀, 0116♂, Rouku; 0247♂, Mari; 0257♂, Morehead; 0273-4♀, Mata.

Notes: This common species was collected from coconut palms, banana trees, a staghorn fern, and wooded areas in general. A female (0082) caught in April 1973 was almost at the termination of her pregnancy.

Nycticeius sanborni (Troughton)

Sanborn's evening bat

Specimens:— Skins and skulls: 0031-3♂, 0034♀, Dimisisi; 0163-4♂, Bula.

Notes: All these specimens were collected from houses in native villages.

Order RODENTIA

Family Muridae

Hydromys chrysogaster beccarii Peters

Common water rat

Specimens:— Skins and skulls: 0272♂, Morehead; 0301♂, 0303♂, Mibini.

Pseudomys delicatula Gould

Native mouse

Specimens:— Skins and skulls: 0048♂, 0120♂, 0260♂, 0286-7♀, 0290♂, 0292♀, Morehead; 0302♂, Mibini. In spirit: 0325♂, Morehead.

Notes: This species is the first recorded for Papua New Guinea. It appeared to be fairly common and was collected in tall mixed savannah using pit traps. This is the second genus from the typically Australian subfamily Pseudomyinae to be found in New Guinea, the first being *Conilurus* (Schodde and Calaby, 1972).

Melomys lutillus muscalis (Thomas)

Little melomys

Specimens:— Skins and skulls: 0009♂, 0075♀, 0084♂, 0248-9♀, Morehead; 0025-6♀, 0142♂, 0307♀, 0321-2♂, 0323♀, Mibini; 0028♂, Tonda; 0035-7♂, 0038♀, 0044-5♂, 0072-3♂, 0097♂, 0100-1♂, 0103♀, 0105♂, 0106♀, 0109-10♂, 0210♂, 0215♂, 0219♂, 0223 unsexed juv., 0224♀, 0226 juv.♂, 0232♀, Wando; 0062 unsexed, Mari; 0122♂, Uparua; 0162♀, 0170♂, Bula; 0182♂, 0185♂, 0188-90♂, Tais.

Notes: This very common mouse was collected over most of the survey area. A female caught in April 1973 was pregnant with three foetuses (0075).

Melomys rufescens niviventer Tate

Rufescent melomys

Specimens:— Skins and skulls: 0179♂, 0267♂, 0269♀, Bula; 0218♀, 0220♂, Wando. In spirit: 0308♂, 0309 juv.♂, Mibini. Skull only: 0003♂, Mibini.

Uromys caudimaculatus aruensis Gray

Mottle-tailed tree rat

Specimens:— Skins and skulls: 0053♀, 0305♀, Mibini. Skulls only: 0005♀, 0313♀, Mibini; 0335 unsexed, Bimadebun. In spirit: 0310♂, Mibini; 0329 juv.♀, 0330-1♂, Bimadebun.

Rattus rattus (Linnaeus)

House rat

Specimens:— Skins and skulls: 0133♀, 0275♀, 0306♀, Morehead.

Notes: All specimens of this introduced rat were collected in the government warehouse at the Morehead Patrol Post.

Rattus sordidus (Gould)

Dusky field rat

Specimens:— Skins and skulls: 0054♂, Dimisisi; 0074♂, 0085 juv.♂, 0092 unsexed juv., 0095♂, Morehead; 0121 juv.♂, 0124 unsexed juv., Uparua; 0304♂, Mibini. Skull only: 0007 unsexed, Morehead.

Rattus leucopus (Gray)

Southern spiny rat

Specimens:— Skins and skulls: 0015♀, 0016-7♂, 0093♂, 0255♀, 0258♀, 0259 unsexed, 0299♀, Morehead; 0018♀, 0022♀, Dimisisi; 0027♂, 0029♀, 0129♂, Tonda; 0068♂, 0099♀, 0217♂, Wando; 0165♀, 0172♂, 0178♀, Bula. Skull only: 0002♀, Morehead. In spirit: 0337♀, Bula.

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Conilurus penicillatus randi Tate & Archbold

Brush-tailed rabbit rat

Specimen:— In spirit 0341 ♀, Morehead.

Notes: This subspecies was represented previously by only one other specimen, caught by Tate in 1936. This recent specimen was caught in an Elliot trap baited with pieces of casava, coconut, and a ball of oatmeal-honey mixture. The trap was set in tall mixed savannah.

Order CARNIVORA

Family Canidae

Canis familiaris Linnaeus

Domestic dog

Specimens:— none

Notes: In 1973 dogs from the villages were just beginning to become feral and form small packs on the Bula Plains. They preyed mainly on the large rusa deer herd found there.

Order ARTIODACTYLA

Family Suidae

Sus scrofa papuensis Lesson & Gasnot

Domestic pig

Specimens:— none

Notes: The feral pig was present throughout the survey area and was the most sought after food of native villagers.

Family Cervidae

Cervus timorensis Blainville

Rusa deer

Specimens:— none

Notes: This species was introduced at Merauke about 1920 by the Dutch (Downes, 1969), and has since spread over most of the Transfly. These animals are found mainly on the grassland strips bordering the rivers, and on the Bula plains.

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Two new species of *Sminthopsis* Thomas (Dasyuridae: Marsupialia) from northern Australia, *S. butleri* and *S. douglasi*

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ABSTRACT

Two new species of *Sminthopsis* are described; *Sminthopsis butleri* n. sp. from northern Western Australia and Cape York, and *Sminthopsis douglasi* n. sp. from northern central Queensland, in the watershed areas of major rivers draining north into the Gulf of Carpentaria. The distribution of *S. butleri* is probably a relict of a formerly (or perhaps extant but unknown) wider range. It is most closely related to *Sminthopsis macroura* (Gould). *S. douglasi* is a very rare and vulnerable species, and may be endangered. It is the second largest species of Dunnart and is closely related to *Sminthopsis virginiae* (Tarragon). Its large size may be the result of character displacement, a reaction to the sympatric, smaller, but morphologically similar *S. macroura* (Gould).

INTRODUCTION

In the course of preparing a revision of the genus *Sminthopsis*, it became evident that two distinct, but unnamed species were represented in existing collections. Specimens of one of these (*Sminthopsis butleri*) were originally collected by Mr A. S. Meek in 1898, from Cape York, Queensland, and more recently by Mr W. H. Butler, from the Kimberley region of Western Australia. The other species (*Sminthopsis douglasi*) is based on specimens collected from north central Queensland by Mr M. Browne in the 1930s.

Having mistakenly assumed that my descriptions of these species would be published earlier than their general reviews, I made the results of my studies on *Sminthopsis* available to several colleagues. This inadvertently resulted in the publication as *nomina nuda* of the two names established in the present paper (e.g. Kirsch 1977).

Terminology of molar and cranial morphology follows Archer (1976a and b); that of tooth number, Archer (1978); and that of pedal morphology, Archer (1977). Selected aspects of this terminology are shown in Figs. 1-2. Measurements

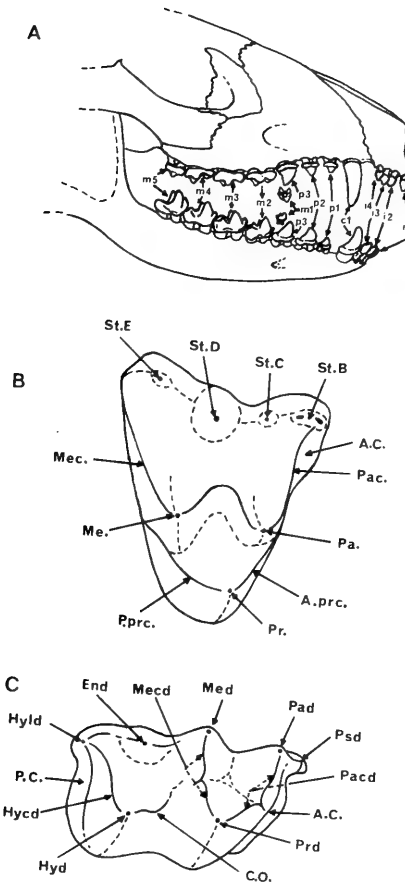


FIG. 1. Terminology of the dentition and molar crowns.

- A. Right lateral view of the rostrum and dentary of a *Sminthopsis* (*S. virginiae*).
- B. Right upper fourth molar (RM⁴) of *S. douglasi*.
- C. Right lower fourth molar (RM₄) of *S. douglasi*.

Abbreviations as follows: A, i = incisor, c = canine, p = premolar, and m = molar; B, A.C. = anterior cingulum, A. prc. = anterior protocrista, Me. = metacone, Mec. = metacrista (more specifically postmetacrista), Pa. = paracone, Pac. = paracrista (more specifically preparacrista), Pr. = protocone, P. prc. = preprotocrista, St. B — E = stylar cusps B to E; C, A.C. = anterior cingulid (or precingulid), C.O. = cristid obliqua, End = entoconid, Hycd = hypocristid, Hyd = hypoconid, Hyld = hypoconulid, Mecd = metacristid, Med = metaconid, Pacd = paracristid, Pad = paraconid, P.C. = posterior cingulum, Prd = protoconid, Psd = parastylid.

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are the same as those defined in the revision of *Antechinomys* (Archer 1977). Abbreviations of institutions are as follows: BM, British Museum (Natural History); B, Butler collection in the Western Australian Museum; J or JM, Queensland Museum; WAM, Western Australian Museum.

The thirteen species of *Sminthopsis* (placed in two sugenera) recognized in the revisionary work in preparation are as follows: *S. murina* (Waterhouse including as junior synonyms *albipes* Waterhouse, *fuliginosa* Gould, and *tatei* Troughton; *S. ooldea* Troughton; *S. leucopus* (Gray), including the junior synonym *ferruginifrons* Gould, *mittelli* Krefft, and *leucogenys* Higgins and Petterd; *S. virginiae* (Traugott), including the junior synonyms *nitela* Collett, *rufigenis* Thomas, *lumboltzi* Iredale and Troughton, and *rona* Tate and Archbold; *S. macroura* (Gould), including the junior synonyms *froggatti* Ramsay, *larapinta* Spencer, *stalker* Thomas, and *monticola* Troughton; *S. hirtipes* Thomas; *S. granulipes* Troughton; *S. psammophila* Spencer; *S. longicaudata* Spencer; *S. crassicaudata* (Gould), including the junior synonyms *centralis* Thomas, and *ferruginea* Finlayson; *S. butleri* Archer (the present work); *S. douglasi* Archer (the present work); *S. (Antechinomys) laniger* (Gould).

SYSTEMATICS

Sminthopsis butleri n. sp.

TYPE SPECIMEN: Holotype: WAM M7158, skull and carcase in alcohol, adult female, collected by Mr W. H. Butler, 14 December 1965.

TYPE LOCALITY: Kalumburu (Lat. 14°15'S, Long. 126°40'E, northern Western Australia (Fig. 5)).

DIAGNOSIS: A medium-sized species of *Sminthopsis* (Fig. 4A and B) that differs from *S. murina*, *S. leucopus* and *S. ooldea* in having a vague head-stripe, a conspicuously enlarged and unstriated apical granule on each interdigital pad, and long premaxillary vacuities. It differs from *S. psammophila* in being smaller, in lacking a crest on the tail, and in having non-granular terminal pads on the digits. It differs from *S. macroura* and *S. douglasi* in having a thin tail, in lacking entoconids on M₂ to M₄, and in having relatively short premaxillary vacuities. It differs from *S. virginiae* in being smaller, lacking rufous cheeks, lacking entoconids on M₂ to M₄, and in having relatively short premaxillary vacuities. It differs from *S. crassicaudata* in having a thin tail, a lack of entoconids on M₂ to M₄, and an enlarged apical granule on the interdigital pads. It differs from *S. longicaudata* in having a tail that is less than twice the nose-vent length, a relatively small alisphenoid tympanic wing, a lack of elongate striated apical granules on the interdigital pads, and a lack of striations on the terminal pads of the digits. It differs from *S. hirtipes* in having a thin tail, relatively long premaxillary vacuities, non-granular terminal pads of the digits, a relatively small alisphenoid tympanic wing, and in lacking hair on

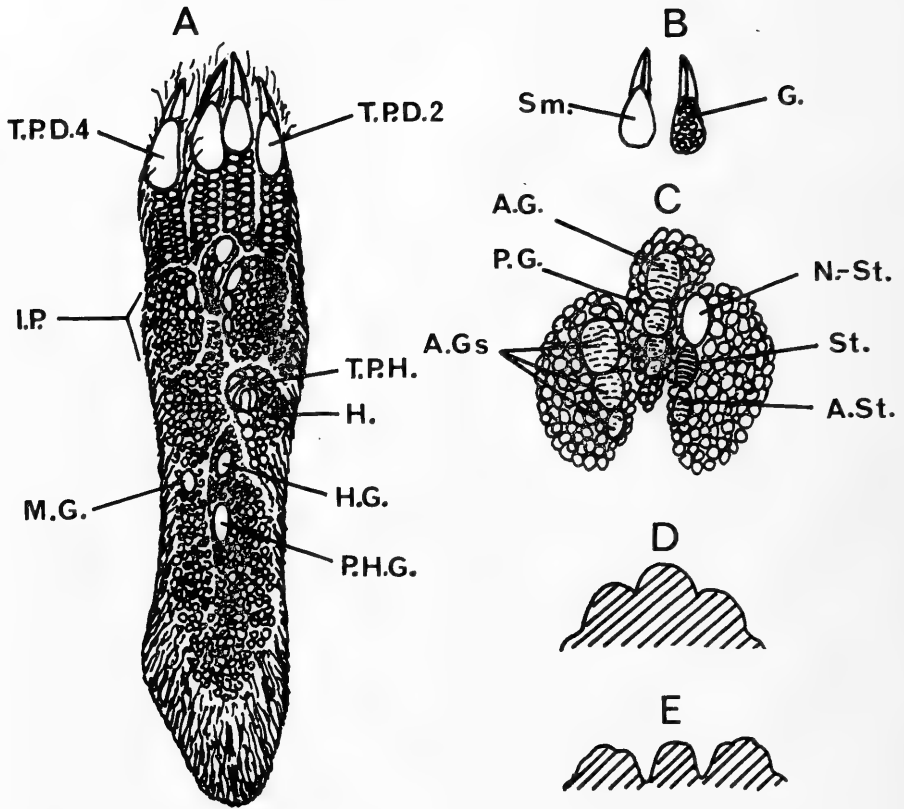


FIG. 2. Terminology for the hind foot of species of *Sminthopsis*. Some features are not present in *S. douglasi* or *S. butleri* (e.g. the post-hallucal granule) but are mentioned in regard to differentiating these from other species in the genus. A, right hind foot, plantar view. B, Terminal digital pads and claws to illustrate alternative conditions of the skin surface. C, the interdigital pads to illustrate terminology and alternative conditions (shown on interdigital pad 1 in this figure) of apical pad surfaces. D, transverse section through the interdigital pads of a species in which the pads are fused towards their top. E, the same as D, but in a species whose pads are unfused or separate to their bases. Abbreviations for A-C are as follows: A.G. = apical granule; A.Gs = row of apical granules containing (in the case illustrated) three apical granules; A. St. = apparently striated appearance of apical granule surface; G. = granular condition of skin surface; H = hallux (the first digit); H.G. = hallucal granule; I.P. = interdigital pads (three); M.G. = metatarsal granule; N-St. = Non-striated (or smooth) appearance of apical granule surface; P.G. = proximal granules (granules adjacent to apical granules); P.H.G. = post-hallucal granule; Sm. = smooth (non-granular) appearance of skin surface; St. = striated surface of apical granule; T.P.D. 2-4 = terminal pads of digits two to four; T.P.H. = terminal pad of hallux.

the interdigital pads of the hind-feet. It differs from *S. granulipes* in having a thin tail, non-granular terminal pads on the digits, an enlarged apical granule on each hairless interdigital pad, a relatively crowded premolar row, and wider molars.

DESCRIPTION: Tail: The tail is invariably thin and about equal in length to the nose-vent length.

Hind foot: The hind foot has three interdigital pads that are united at their common base. Each interdigital pad has a medium row of granules each of which become progressively larger towards the distal end of each pad. Each row culminates in a large apical granule. Of five alcohol-preserved specimens, only one (B1937) exhibits fusion of an apical granule with the proximal granules (on the left and right fourth interdigital pads, the apical granule is fused with a proximal granule and there is also an imperfect fusion involving apical and proximal granules of the left and right second interdigital pads). On some interdigital pads (e.g. the left and right fourth of WAM M7158 and B1941), the apical rows are not as long and do not involve as many granules as in other specimens (e.g. the third of B1943 and WAM M7158). The presence of the hallucal granule is variable, being clearly differentiated for example in B1943, B1941 and B1937 but virtually absent on the right foot of B1937 and both feet of WAM M7158. No granules exhibit actual ridges on the surface of the pads but some apical and proximal granules (e.g. B1941) have apparent striae. The hallux does not extend forward far enough to touch the second interdigital pad.

Nose: The nose has a medial groove which does not extend to the top of the naked rhinarium. A narrow, hairless, ventrolateral rim is present.

Nipple number: Specimen WAM M7158 has eight distinct nipples.

Pelage: A relatively dark mid-dorsal head-stripe extends from an area about midway between the nose and the anterior edge of the eye to between the ears, behind which it merges with the color of the back. A dark ring occurs around each eye but does not form part of the lateral face stripe. The very light colour of the belly extends onto the flanks between the fore and hind legs and along the base of the cheeks beneath the ear. Ridgway (1912) colours for a dry skin (WAM M7156) and an alcohol carcase (WAM M7158) are as follows: Above the eye, vinaceous-Buff to Avellaneous (M7156) or Pale Ochraceous-Buff (mixed) (M7158); middle of the back, Buffy brown to Drab Mouse Gray (former as tips of hairs) (M7156) or Blackish Brown (M7158); flank, Pale Ochraceous salmon to Vinaceous-Buff (M7156) or Light Buff (M7158); belly, white to Ivory yellow (M7156) or paler than Massicot yellow (M7158).

Dentition: The I^1 is the tallest upper incisor and is set off from I^2 by a diastema. Upper incisor crown heights increase posteriorly from I^2 to I^4 . The I^4 has a small (B1995) or absent (WAM M7156) posterior lobe. A diastema occurs between I^4 and C^1 . The C^1 has posterobuccal and posterolingual cingula, a small posterior cin-

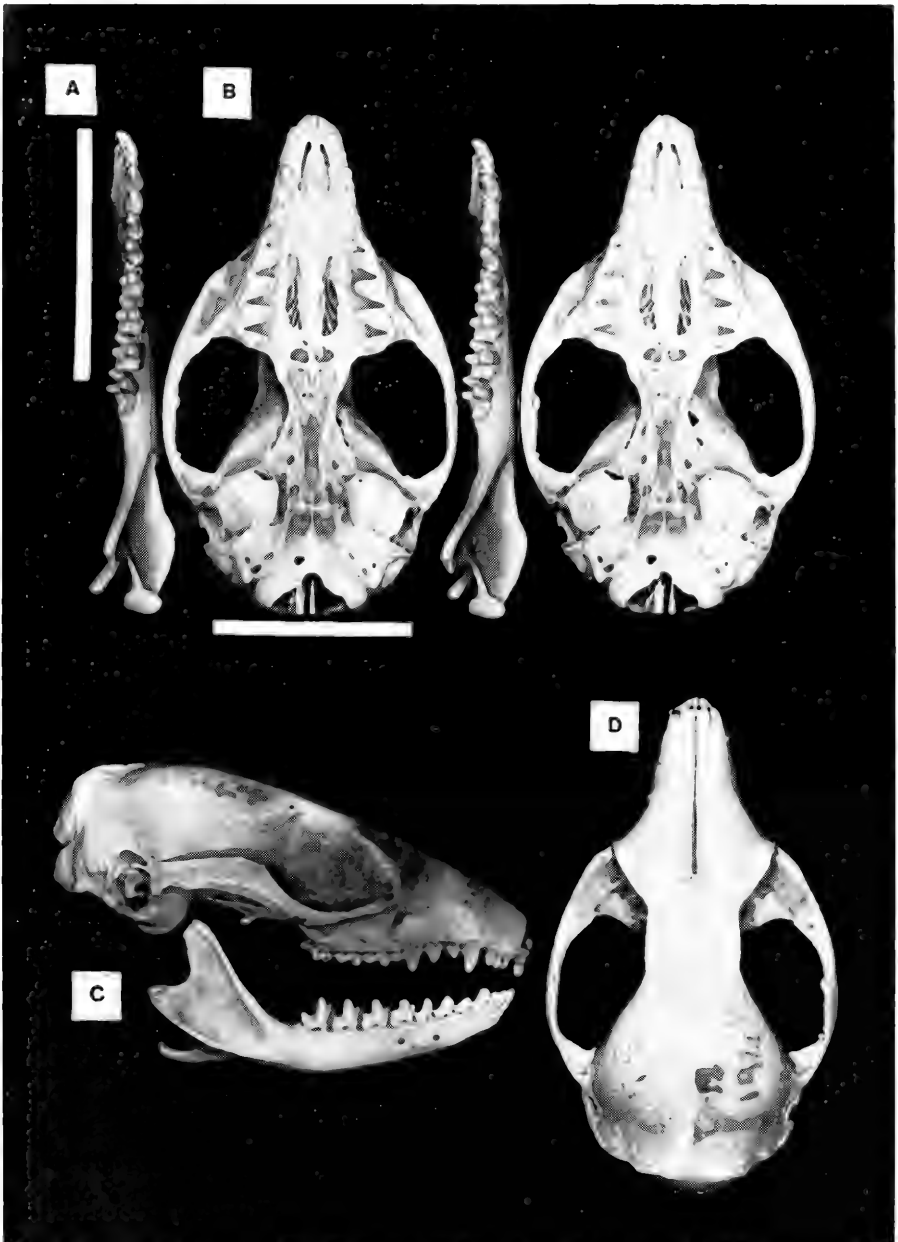


FIG. 3. A-D *Sminthopsis butleri* skull and right dentary of the holotype WAM M7158, Kalumburu, Western Australia. The white line by A represents 10 mm for A. The white line below B represents 10 mm for B-D. A and B are presented as stereopairs.

gular cusp, and is caniniform although its crown height is shorter than that of P^3 . The P^1 is slightly shorter in crown height than P^2 and P^2 is conspicuously shorter in crown height than P^3 . Lingual and buccal cingula on P^1 to P^3 are incomplete at the base of the paraconid. Posterobuccal cingula on P^1 to P^2 are variably rugose with smaller irregular cusps. The M^1 (e.g. B1995) is three-rooted with three principal cusps, the paracone, metacone and stylar cusp D. There is also a very reduced protocone and possibly the homologue of stylar cusp B on the anterobuccal cingulum. A complete anterior cingulum is present from the preprotocrista to the parastylar corner of the M^1 . The M^1 postmetacrista is large but the preparacrista is not a prominent crest. The paracones of M^2 to M^5 increase in height posteriorly. The protocones of M^2 to M^4 are subequal in height to each other, as are the metacones. The protocone of M^5 is the smallest of the upper molars. Stylar cusp D is largest on M^2 and decreases in size posteriorly being miniscule or absent on M^5 . Stylar cusp A is indistinct on M^2 to M^5 but may be distinguishable on M^2 (e.g. WAM M7156). Stylar cusp A is defined by the intersection of an anterior crest from stylar cusp B and the anterior molar cingulum. Stylar cusp C is not present. An anterior cingulum is incomplete except on M^2 where it is sometimes complete (e.g. B1995). Rarely, an anterior cingulum is complete on M^3 (e.g. B1939). The paracrista of M^2 is well-formed and either extends buccally (e.g. B1995) or anterobuccally (e.g. WAM M7156) to the paracone. The preparacrista length increases posteriorly from M^2 to M^5 . The postmetacrista of M^2 and M^4 are subequal in length and shorter than the postmetacrista of M^3 . The I_1 is taller-crowned than I_2 . The I_3 has a small posterior lobe. The C_1 is caniniform, subequal in crown height to P_3 , has a small posterior lingular cusp, a complete lingual cingulum, and an incomplete buccal cingulum. The P_1 is shorter-crowned than P_2 which is shorter-crowned than P_3 . Lingual and buccal cingula of P_1 to P_2 are small and generally incomplete. The P_3 lacks a buccal cingulum but has a lingual cingulum. The M_1 (e.g. B1995) is two-rooted with the protoconid as the only main cusp. There is also a small anterior cusp homologous either with the paraconid of M_2 or the anterior lingular cusp of the anterior premolars, and a small posterior cusp homologous either with the hypoconulid of M_2 or the posterior lingular cusp of the anterior premolars. A swelling between the posterior cusp and the protoconid may be homologous with a hypoconid. The paraconids of M_2 to M_5 increase in height posteriorly. The metaconids of M_2 to M_5 are subequal in height. The protoconids increase in height from M_2 to M_5 . The hypoconids of M_2 to M_4 are subequal in height and taller than the hypoconid of M_5 . The entoconids are tiny on M_2 to M_4 and absent on M_5 . On one specimen (B1995) a tiny metastylid appears on M_2 . The paracristids of M_3 to M_5 are subequal in length and longer than the paracristid of M_2 . The metacristids of M_2 to M_4 increase in length posteriorly from M_2 to M_4 . The metacristid of M_5 is subequal to that crest in M_3 . The trigonid is narrower than the talonid on M_2 , subequal in width on M_3 , and wider than the talonid on M_4 and M_5 .



A

FIG. 4. A-B *Sminthopsis butleri*, Holotype photographed alive (photographs by W. D. L. Ride).



B

Skull and dentary (see Fig. 3 A-D): the skull is relatively brachycephalic with a short deep rostrum and broad zygomatic arches. It is domed posteriorly and, in older individuals, has well-developed sagittal and nuchal crests. A longitudinal medium depression occurs in the region of the naso-frontal suture. The interorbital region has pronounced postorbital swellings but no postorbital processes. There are normally two lacrimal foramina on each orbital rim (except on one side of WAM M2155, where there is only one). The alisphenoid tympanic wing is only slightly enlarged, leaving the ectotympanic ring broadly exposed. The periotic tympanic wing is little developed compared with other species such as *S. hirtipes*. The foramen pseudovale is large. The transverse canal foramen is relatively large but smaller than the foramen rotundum. The opening to the eustachian canal is large, as is the internal jugular vein and the posterior lacerate foramina. The entocarotid canal is open ventrally but well-developed. The condylar foramina (including the hypoglossal foramen) is single or multiple. The premaxillary vacuity extends posteriorly usually to the level of the anterior root of P² (e.g. B1995) or the posterior root of P² (e.g. WAM M7156). Usually (e.g. B1995) several small interdental fenestrae occur between adjacent upper molars. The maxillary vacuity extends forward to the level of the anterior end of M². The distance between the articular condyle of the dentary and the tip of the ascending ramus is slightly shorter than the distance from the articular condyle to the tip of the angular process. The masseteric fossa is large. The symphysis extends posteriorly to the level of the posterior edge of P₂.

DISCUSSION: This species has been the subject of serological analysis by Kirsch (1967, as *S. nitela*, and 1977, as *S. butleri*) who also examined sera of the following species: *S. macroura* (as *S. larapinta*) from Doomadgee Mission, Queensland; *S. murina* from Busselton, and Scott River, Western Australia; *S. granulipes* from Western Australia (including a specimen from Gingin); and *S. crassicaudata* from Wongan Hills, Western Australia. He considers all of the species to be serologically differentiable at the species level. Bannister (1969) refers the Kalumburu specimens to *Sminthopsis* sp. cf. *nitela*. Ride (1970) considers the Kalumburu specimens to possibly represent *S. virginiae* (as *S. nitela*). However, the virtual absence of entoconids, rufous cheeks or comparable foot structure serve to distinguish *S. butleri* from *S. nitela*. The affinities of *S. butleri* probably lie with *S. macroura*.

The two specimens of *S. butleri* in the British Museum (BM 1939.3243 ♂ and BM 1939.3245 ♀) were collected by Mr A. S. Meek on 22 July, 1898, and were given to the British Museum as part of the Rothschild Bequest. No details of habitat or other information were recorded. The locality is given on the labels simply as "Cape York". However, Parker (1973: 121-2) has published further information about aspects of Meek's itinerary. According to letters written by Mr A.S. Meek, he indicated at least an intention to travel from Cooktown to "Thursday Island and Somerset way" for six weeks from about 22 July to 2 September 1898.

Assuming he stuck to his anticipated schedule, it seems most probable that the specimens of *S. butleri* collected by Meek on 22 July must have come from very near Cooktown.

The apparent absence of the species between the Kimberleys and Cape York (Fig. 5) is unique among dasyurids otherwise present in these two areas. I would predict the species will eventually be found (if only to have formerly occurred) in Arnhem Land. It is not at present known to occur in Cape York despite several recent surveys.

Mr W. H. Butler (p. 568 in his unpublished field notes in the Western Australian Museum Library) gives the Aboriginal name of this species as "Moonjol".

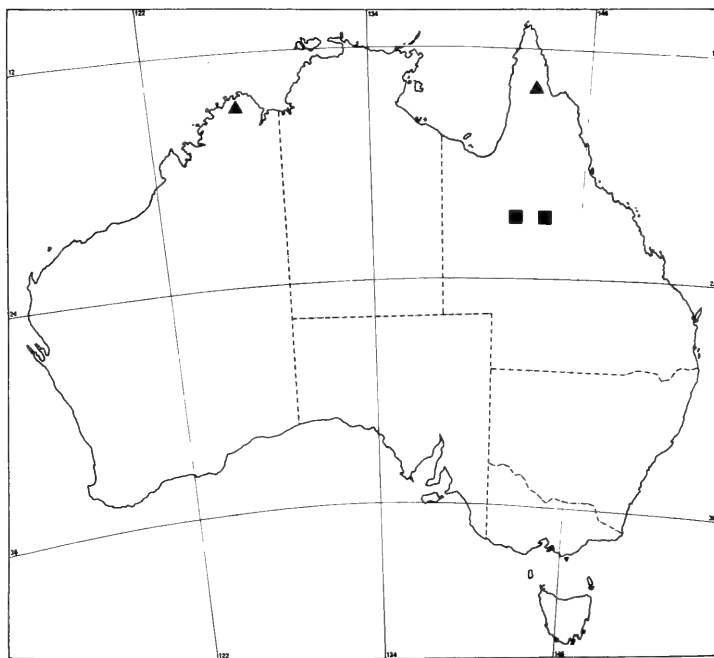


FIG. 5. Localities for *Smynthopsis butleri* (triangles) and *S. douglasi* (squares) in Australia. Queensland locality for *S. butleri* (based on Meek's specimens) is only approximate (see text).

HABITAT AND REPRODUCTION: Mr W. H. Butler's field notes state that he collected "... north of the King Edward River about 4 miles from the Longini landing for cargo" (Fig. 5). Specimens include one male (which I have not seen) and two females (M7158 and B1995). One was "... caught on blacksoil sandplain

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junction at bottom of airstrip . . ." and two (including B1995) were removed from ". . . flood debris at back of Mission". The blacksoil plain and sand plain were ". . . heavily vegetated with eucalypt and grass". At the time of collection there were heavy rains in the area, producing as much as 181 mm in two days. The holotype, WAM M7158 had seven pouch young (including WAM M7155-7) at the time of collection, 12 December 1965. Paratype B1995 is a juvenile that was caught on its own, 39 days after WAM M7158 was caught with the seven pouch young. The holotype and her seven juveniles were sent live to Perth where they were maintained live until 16 May, 1966, when they were used to provide sera for the studies of Kirsch (1967). For this reason, although the juveniles were collected earlier than paratype B1995, they are older in developmental age and larger in size (see Tables 1-2).

REMARKS ABOUT THE HOLOTYPE AND PARATYPE: The holotype consists of a well-preserved carcase and relatively little-damaged skull and dentaries. The paratype, B1995, a juvenile female, was collected by Mr W. H. Butler at Kalumburu, from floodwater debris, on 20 January, 1966. At the time of collection it weighed 3.9 grams. The M1 is still in situ and the M5 is erupting.

ORIGIN OF NAME: This species is named in honour of Mr W. H. Butler. Mr Butler, the well-known naturalist and conservationist, has collected many small mammals in addition to the holotype of *S. butleri*, previously unknown to science.

Sminthopsis douglasi n. sp.

HOLOTYPE: Queensland Museum J5173, skull and carcase in alcohol, juvenile female, collected by Mr M. Browne, registered in the Queensland Museum on 24 July, 1931.

TYPE LOCALITY: Julia Creek (Lat. 20°40'S, Long. 141°40'E) north central Queensland, in the watershed of the Cloncurry River (Fig. 5).

DIAGNOSIS: Very large species of *Sminthopsis*, larger than all species except *S. psammophila*. Morphologically it is similar to *S. virginiae* but differs from the latter in being larger and in having a very stout or incrassated tail. It differs from most other species of *Sminthopsis* in lacking a continuous anterior cingulum on the upper molars (some *S. virginiae* also appear to lack a continuous anterior cingulum). It differs from *S. murina*, *S. ooldea* and *S. leucopus* in being larger, in having large entoconids on M₂ to M₄, a pronounced dark stripe on the forehead, and a premaxillary vacuity that does not extend posteriorly beyond a point level with the rear of the C¹ alveolus. It differs from *S. granulipes* and *S. hirtipes* in being larger, in having a thinner tail, rufous cheeks, large entoconids on M₂ to M₄, enlarged apical granules on the hairless interdigital pads, and non-granular terminal pads on the toes. It differs from *S. psammophila* in being smaller, having no crest

Table 1: Cranial and dental measurements (mm) of *Sminthopsis butleri* and *S. douglasi*

SPECIMEN	BL	ZW	OBW	IBW	C-M ⁵	M ²⁻⁵	M ²⁻⁴	R-LM ⁴	IO	IPVD	DL	I-M ₆	M ₂₋₅
WAM M7158 ♀	22.8	14.6	9.4	3.2	9.2	4.9	4.3	7.7	4.4	2.9	18.4	10.1	5.6
WAM M7157 ♂	21.7	13.9	9.0	3.5	8.9	5.1	4.7	7.8	4.2	2.2	17.6	10.3	6.2
WAM M7155	20.6	—	9.0	2.9	8.6	4.8	4.6	7.4	4.1	2.4	16.6	10.0	6.0
WAM M7156 ♂	21.2	—	8.6	2.8	8.8	5.3	4.7	7.3	4.5	2.2	—	—	6.2
B 1939	20.1	—	8.7	2.8	8.4	5.0	4.7	7.4	4.1	2.4	—	—	6.2
B 1995	20.7	12.6	8.7	3.1	—	—	4.5	7.3	4.4	2.6	16.3	10.5	6.1
BM 1939.3245 ♀	22.0	13.0	8.9	3.6	9.0	5.1	4.1	7.4	4.3	3.7	17.8	10.2	5.5
BM 1939.3243 ♂	—	15.3	—	—	9.8	5.2	4.5	8.3	4.5	4.4	20.5	11.2	5.7
J 5173 ♀	25.2	15.9	10.6	3.8	—	—	6.2	9.7	5.1	5.2	20.3	13.7	8.0
J 5459 ♀	26.7	16.9	10.7	4.0	11.8	6.8	5.9	9.8	5.1	5.6	22.0	13.6	7.8
AM M2172 ♂	29.8	17.6	11.3	—	13.0	7.1	6.2	10.4	5.2	—	23.5	14.9	8.2

SPECIMEN	M ₂₋₄	C-AP	C-AR	AGE	SPECIES	LOCALITY
WAM M7158 ♀	4.1	5.5	4.4	Adult	<i>S. butleri</i>	Kalumburu, W.A.
WAM M7157 ♂	4.6	5.0	4.4	Subadult	"	"
WAM M7155	4.5	5.0	4.2	"	"	"
WAM M7156 ♂	4.5	5.0	4.0	"	"	"
B 1939	4.6	5.2	3.8	Juvenile	"	"
B 1995	4.5	4.7	3.7	Adult	"	"
BM 1939.3245 ♀	4.1	4.9	3.8	"	"	Cape York, QLD
BM 1939.3243 ♂	4.3	5.9	4.9	Juvenile	<i>S. douglasi</i>	Julia Creek, QLD
J 5173 ♀	6.1	6.0	5.0	Adult	"	"
J 5459 ♀	6.0	6.3	5.6	"	"	"
AM M2172 ♂	6.1	6.7	5.6	"	"	Richmond, QLD

BL, basicranial length; ZW, maximum outside zygomatic width; OBW, distance between edges of both alisphenoid hypotympanic sinuses; IBW, distance between internal edges of alisphenoid hypotympanic sinuses; R-LM⁴, distance across palate from buccal sides of the left and right M⁴; IO, minimum interorbital width across top of skull; IPVD, distance between posterior edge of the premaxillary palatal vacuity and the anterior edge of the maxillary palatal vacuity; DL, dentary length; C-AP, distance between the dorsal surface of the articular condyle of the dentary and the tip of the angular process; C-AR, distance between the posterior edge of the condyle of the dentary and the anterior edge of the ascending ramus.

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Table 2: External measurements (mm) of *Sminthopsis butleri* and *S. douglasi*

SPECIMEN	Nose-vent (HB)	Tail-vent (TV)	Hind foot (without claws)	Ear (from notch)	AGE	SPECIES	LOCALITY
WAM M7158 ♀	88.0	90.0	16.0	17.2	Adult	<i>S. butleri</i>	Kalumburu
B 1995 ♀	69.0	72.0	16.0	15.0	Juvenile	" "	" "
WAM M7157 ♂	82.0	72.0	19.0	15.0	" "	" "	" "
WAM M7156 ♂	75.0	79.5	16.3	14.0	" "	" "	" "
J 5173 ♀	92.3	84.7	21.0	16.0	Juvenile	<i>S. douglasi</i>	Julia Creek
J 5459 ♀	—	105.0	22.2	—	Adult	" "	" "

on the tail, having rufous cheeks, large entoconids on M_2 to M_4 , smooth non-granular terminal pads on the toes, and a distinct mid-forehead stripe. It differs from *S. crassicaudata* in being larger, in having a thinner tail, enlarged apical granules on the interdigital pads, entoconids on M_2 to M_4 that are clearly not contacted by the hypocristid, a premaxillary vacuity that extends no further posteriorly than a point level with the rear of the C^1 alveolus, and a P_3 that is conspicuously larger than P_2 . It differs from *S. macroura* in being larger, in having a thinner tail, rufous colouring on the cheeks, and commonly a continuous anterior cingulum on the upper molars. It differs from *S. longicaudata* in having a tail-vent length that is less than twice the nose-vent length, non-striated to barely striated terminal pads on the digits and the apical granules of the interdigital pads, large entoconids on M_2 to M_4 , caniniform canines; and a premaxillary vacuity that does not extend posteriorly beyond a point level with the rear of the C^1 alveolus. It differs from *S. butleri* in being larger, having large entoconids on M_2 to M_4 , and in having rufous cheeks.

DESCRIPTION: Tail: The tail is approximately equal to, or slightly longer than, the nose-vent length. Incrassation varies from being stout (paratype) to conspicuously swollen (holotype).

Ear: The ear is relatively large, with a markedly curled external edge on the supratragus, and with rufous hairs on the postero-internal and ventral margins of the pinna of the holotype.

Hind foot: The interdigital pads are fused near their bases. The apical granules are enlarged, elongate and striate. The second and fourth pads appear in the holotype to have slight ridges on the surface of the granules although this may be an artifact of alcoholic dehydration. All interdigital pads of the paratype have striate apical granules with ridges on the surfaces of these granules. The apical granule of the left third interdigital pad of the holotype is not clearly striate. There is no enlarged hallual granule in the holotype although a slightly enlarged hallual granule occurs in the paratype. Metatarsal granules are not present. Hair on the

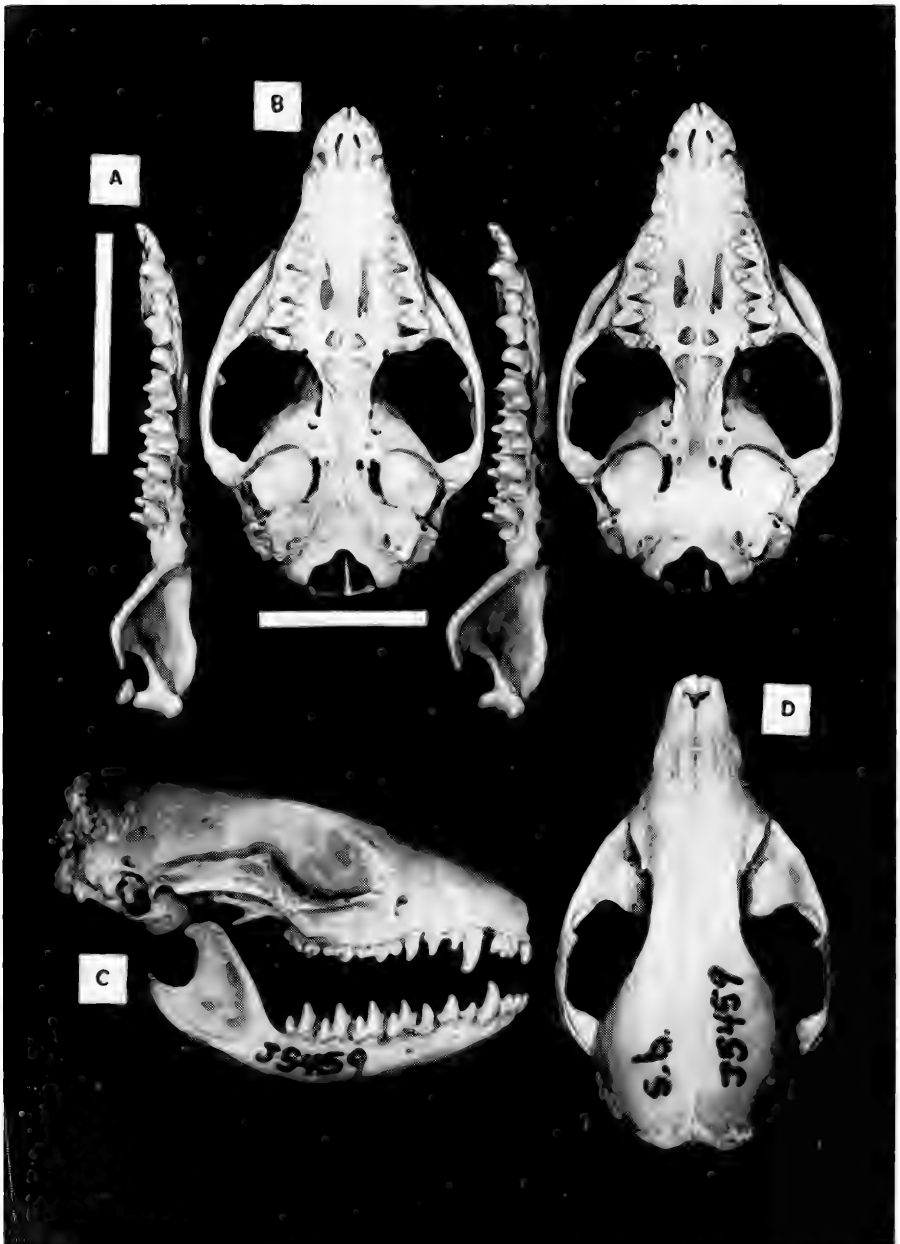


FIG. 6. *Sminthopsis douglasi*, skull and right dentary of the Holotype J5495, Julia Creek, Queensland. The white line by A represents 10 mm for A. The white line below B represents 10 mm for B-D. A and B are presented as stereopairs.

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feet covers the heel and extends diagonally across the foot. The terminal pads of the digits are not clearly striate in the holotype but suggestions of striae occur on the terminal pads of the paratype.

Pelage: The general colour is similar to *virginiae*, with rufous colouring on the cheeks and surrounding the eyes (except around the anterior margin). In the holotype the rufous colouring extends anteriorly just beyond the eye but in the paratype rufous colouring extends to the rhinarium. A dark brown mid-dorsal head-stripe extends in the holotype as far anteriorly as the rufous colouration. In the paratype the head-stripe extends to the rhinarium. Although both specimens are alcohol-preserved carcasses, rufous hairs appear in many areas in the postcranial pelage, e.g. behind the ears, the forearm, beneath the base of the tail, and around the ankle. Ridgway (1912) colour description for the only dry skin, referred specimen AM M2172 are as follows: head stripe, Seal Brown; above the eye, Tawny Olive; middle of the back, Bistre to Vandyke Brown; flank, Wood Brown to Ochraceous-Buff, belly, Olive-Buff.

Nose: The hairless rim is restricted to the extreme ventral margins of the rhinarium. The medial groove in the holotype extends to (or stops just short of) the top of the rhinarium. The nose is bicoloured, being caramel at the base to dark reddish-brown at the top. The nose of the paratype is damaged but does not conflict with this description.

Nipple number: The holotype has eight relatively undeveloped nipples. The paratype has seven enlarged and elongate nipples. An eighth appears to be missing from the right side.

Dentition: The I^1 is conspicuously larger than I^2 and is set off from that tooth by a diastema. The I^4 is slightly larger than I^2 , and a slight increase in incisor crown size occurs from I^2 to I^4 . Between I^4 and C^1 is a fossa corresponding with the crown tip of C_1 . The C^1 is considerably less than twice the height of P^3 , and subequal to twice the height of P^1 . There is an increase in premolar size from P^2 to P^3 . Buccal cingula on P^1 to P^3 are continuous, and poorly developed to absent on C^1 . Lingual cingula are present on P^1 to P^3 , except beneath the paracone, and poor to absent on C^1 . Anterior and posterior cingula and small anterior cusps are present on C^1 to P^3 . Small posterior cusps occur on P^1 to P^3 . The M^1 has a large metacone, a small paracone, a basal poorly differentiated protocone, a stylar cusp D (present on the LM^1 but not the RM^1), prominent postmetacrista, no preparacrista, possibly a miniscule continuous anterior cingulum (RM^1), and three roots. Continuous anterior cingula are absent on M^2 to M^4 (although the RM^2 of the paratype may have a miniscule continuous anterior cingulum) and present on M^5 . There are suggestions of a stylar cusp C on M^3 and M^4 . The abnormal nature of stylar cusp C on RM^2 of the holotype and the compressed M^4 of the paratype are described elsewhere (Archer 1975). The postmetacrista of M^4 in the

holotype is shorter than the crown length. The I_1 is the largest lower incisor. The I_2 is larger than I_3 . The I_3 has a very small posterior cusp. The C_1 is larger than P_3 . Premolars increase in size from P_1 to P_3 . Continuous buccal cingula occur on P_1 to P_3 . Anterolingual cingula are absent or tiny on P_1 to P_3 . The buccal and lingual cingula of C_1 are entire in the paratype but poorly developed in the holotype. The tip of the P_3 crown of the holotype is visible beneath M_1 . The M_1 is two-rooted with a protoconid, a topographic homologue of the hypoconulid, and a miniscule anterior cingulum. The entoconids on M_2 to M_4 are large but not in contact with the hypocristids. The talonids of M_2 and M_3 of the paratype are wider than the trigonids, but on M_4 the talonid and trigonid are subequal width as they also are on M_3 of the holotype. An abnormal bifid entoconid occurs on the RM_4 of the paratype (Archer 1975).

Skull and dentaries (See Fig. 6A-D): The lacrimal foramina are single or double, and occur on, or just posterior to, the edge of the orbit. The lacrimal has a variably developed posterodorsal spine. Postorbital processes are not present in the holotype or paratype. A dorsal anteroposterior depression is notable between the frontals. The skulls are mildly domed dorsally (but apparently less so than in *virginiae*). The premaxillary vacuities are short, not reaching a point level with the posterior edge of the canine alveolus. An indentation in the palate of the paratype suggests an incipient posterolateral palatal foramen. The alisphenoid and periotic tympanic wings are poorly developed and broadly expose the ectotympanic ring. The transverse foramen is small. The foramen rotundum is exposed ventrally in the paratype but is partially obscured by a ventral bony shelf in the holotype. The foramen pseudovale is large with posterolateral projections extending out from the basisphenoid portion of the alisphenoid. The entocarotid canal varies in size from short in the paratype to relatively long in the holotype. On the right side of the holotype, entocarotid canal development is such that the entocarotid foramen permits direct dorsoventral observation into the cranial cavity. The basioccipital walls of the internal jugular canal are not vertical. The masseteric fossa of the ascending ramus is broad, with the anterior border of the ascending ramus and the posterior margin of the dentary widely divergent. The angular process of the dentary is stout, short and abruptly tapered.

DISCUSSION: Troughton (1965) refers J5173 and J5459 to *S. virginiae* (as *S. lumboltzi*) without giving reasons. He does not mention the mildly incrassated tails or very large size of these specimens. He also refers another north central Australian specimen, AM M2172 from Wyangarie Station, Richmond, with a markedly incrassated tail, to *S. virginiae*. This specimen is referred here to *S. douglasi*. All three specimens are much larger than *S. virginiae* and have mildly to conspicuously incrassated tails.

S. douglasi appears to be most closely related to *S. virginiae*. Its large size may be a response to the presence of the sympatric and also distantly related *S. macroura*

(e.g. J7680 from Richmond and J11463 from Julia Creek). *S. douglasi* and *S. virginiae* share many cranial, dental, and external characters such as the large and morphologically similar entoconids, small alisphenoid tympanic wings, short premaxillary palatal vacuities, relatively large canines, similar foot pad structure, and caudal incrassation. If competition occurred at some time in the past it might be expected that some form of character displacement would develop, such as the much larger *S. douglasi* (developing from a structurally smaller ancestral form similar to *S. virginiae*).

HABITAT AND REPRODUCTION: The type locality (Fig. 5) and the Richmond area are ecologically different areas from localities inhabited by *S. virginiae*. In particular, the lower rainfall in the Julia Creek and Richmond areas (444-459 mm per year) contrasts with the higher rainfall of areas containing *S. virginiae* (1135 mm or more per year). This more arid habitat may be responsible for the evolution of incrassated tails in *S. douglasi*. Paratype J5459, registered on 24 May 1933, has 6 juveniles attached to its nipples in a well-formed pouch which is dorsoventrally about 1 cm deep. These were removed for determination of the nipple number (7). The juveniles are shrivelled through alcoholic dehydration. The lengths of the heads from the nose to the posterior edge of the occipital, range from 6.0 to 6.4 mm. Because the date of registration cannot be assumed to approximate the date of collection, it is impossible to determine at what time of year the young were born.

MEASUREMENTS: Measurements were recorded in the Queensland Museum catalogue for the holotype at the time of registration as (in mm): HB, 95.0; T, 97.0; HF, 21.0; E, 16.0. The tail measurement was probably made from the dorsal side and not as recommended by Thomas (1888, p. viii) from the vent. The former method is convenient for placental mammals which have a clear cut external boundary between the tail and body, but not for marsupials whose body and tail commonly have no such external boundary. Measurements of the holotype and paratype made during this study are given in Table 2. Because they are made on old alcohol-preserved carcasses whose skulls have been removed, they are only approximations of fresh measurements.

DETAILS OF THE PARATYPE: Paratype J5459 consists of a skull, a damaged carcass in alcohol, and 6 juveniles in the pouch, collected by M. Browne at Garomna, Julia Creek. This is possibly the same locality as that of the holotype, although Garomna is not listed in the Queensland Museum catalogue in regard to the holotype. The registration date given in the Queensland Museum catalogue for J5459 is 24 May 1933. This date may roughly correspond with the collection date, but of this there can be no certainty. An examination of Queensland Museum correspondence for 1931 and 1933 produced no information concerning the acquisition of either the holotype or paratype. Although J5459 is technically an adult, since P3 has erupted, it is a young adult with relatively unworn teeth. Both the holotype and paratype are females and may be expected to be smaller on the

average than males. AM M2172 is a male and has a larger skull, although the teeth are subequal in size.

DETAILS OF THE REFERRED SPECIMEN: AM M2172 represents a young adult male, skin and skull, from Wyangarie Station, Richmond, north Queensland. It was presented by F. L. Berney to the Australian Museum. An old label attached to the skin says "*Sminthopsis* sp. nov. allied to *virginiae*. Central Queensland". A note on the same label in E. Le G. Troughton's hand says "... original label proving that A. A. McCulloch observed distinction, in association with '*virginiae*'. E. Le G.T. 5/11/1963". The skin, even in the dehydrated state, shows a pronounced incrassated tail.

ORIGIN OF NAME: *S. douglasi* is named in honour of Mr A. M. Douglas, one of Australia's foremost naturalists and bushmen. He has spent over twenty years building up and curating collections in the Western Australian Museum and teaching many of his hard-earned skills to colleagues and students.

ACKNOWLEDGEMENTS

Mr. W. H. Butler deserves special thanks for collecting the Kimberley specimens of *Sminthopsis butleri*. Mr. A. M. Douglas also deserves special thanks for spending much of his time with me in the bush, helping me to see things I would otherwise have missed. Mr. J. Bannister (now Director and formerly Curator of Mammals of the Western Australian Museum) kindly permitted study of the Dunnarts collected by Mr. Butler, as well as those already in the Museum's collection. Ms. J. Covacevich (Queensland Museum) and Mr. B. Marlow (Australian Museum) also kindly allowed me to examine specimens of *S. douglasi* in their collections. Mr. A. Easton (Queensland Museum) took the photographs of skulls. Dr. W. D. L. Ride (then Director of the Western Australian Museum) took the photographs of the live *S. butleri*. Ms. D. Thomas (University of New South Wales) typed the manuscript.

Drafts of this paper have been constructively criticised by Dr. W. D. L. Ride, Professors G. G. Simpson and O. Reig, Dr. J. A. W. Kirsch, Mr. H. Van Deusen, Dr. R. H. Tedford and Dr. G. Musser.

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A study of intraspecific variation in the green tree frog *Litoria chloris* (Boulenger) (Hylidae)

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ABSTRACT

The morphological and osteological variation of three disjunct populations of *Litoria chloris* have been subjected to a number of analyses. Interpopulation differences include size of adult, shape of the head and thigh colouration. It is conceivable that the species as now recognised includes more than one taxon. Biological data would confirm or refute a supposition derived from morphometric data.

INTRODUCTION

The importance of a detailed knowledge of intraspecific variation amongst anuran populations as a prerequisite to meaningful interspecific comparisons has been appreciated only recently. Extensive gene flow within a population can produce such variation that the interpretation of character states used in systematic studies can be altered radically.

Trueb (1977) has shown considerable variation in osteological characters within a single population of the tree frog *Hyla lanciformis*, and extensive variations in morphological, osteological and behavioural characters have been shown over an altitudinal gradient in *Hyla lancasteri* (Trueb, 1968). Limited variation in cranial characters within three geographically disjunct populations of *Litoria infrafrenata* was found by Davies (1978).

There exist in Australia instances in which two or more disjunct frog populations exhibit variation in morphological characters, so leading to a degree of uncertainty regarding the taxonomic status of such populations. The hylid frog *Litoria chloris* (Boulenger) is such an example. It occurs in closed rainforests in

Queensland and New South Wales along a narrow coastal strip of some few kilometres wide which extends over one thousand kilometres. Disjunctions within this range are probably of recent origin being correlated with the destruction by European man of coastal rainforest.

Here we record morphological and osteological variation within *Litoria chloris*, together with previously unpublished data on natural history, and attempt to correlate such variation with complementary geographic isolation.

MATERIALS AND METHODS

Abbreviations: A.M. Australian Museum; A.M.N.H. American Museum of Natural History; K.U. University of Kansas, Museum of Natural History; L.A.C.M. Los Angeles County Museum; N.P.W.S. Queensland National Parks & Wildlife Service; Q.M. Queensland Museum; S.A.M. South Australian Museum; U.A.Z. Zoology Department, University of Adelaide; N.P. National Park; S.F. State Forest. Letters following acronyms are departmental registration abbreviations.

Specimens examined: Specimens or series of specimens marked with an asterisk have not been included in the morphological analysis, but are distribution records.

Northern Population: Q.M. J.17109, Atherton; Q.M. J.17110, Crystal Cascades; Q.M. J. 27105-6, Little Forks; Q.M. J.25194-5*, Q.M. J.25258-60, Home Rule Falls, Cooktown; Q.M. J.25278*, $\frac{1}{4}$ mile east of "Granite", Home Rule; N.P.W.S. A.252-3, Longmans Gap; N.P.W.S. A.255-7, Lake Barrine N.P.; N.P.W.S. Q.P.A.026-7, Severin, Boar Pocket; N.P.W.S. N.14292-3, Crater N.P.; N.P.W.S. N.14270-3, N.P.W.S. N.14274-5*, N.P.W.S. N.14276, Palmerston N.P.; N.P.W.S. N.14310-1, Mt. Lewis S.F.; N.P.W.S. N.14162-3, McDowell Range; N.P.W.S. N.14185-6, Mt. Baldy, south-west Atherton; N.P.W.S. N.14298-9*, Lake Eacham N.P.; N.P.W.S. N.28113-4*, Gadgarra S.F.; N.P.W.S. N.14533-43*, Charappa Creek; K.U. 147231*, Tinaroo Creek Road, Mareeba; L.A.C.M. 41136-58*, 50732*, Lake Eacham, east of Atherton; L.A.C.M. 41163*, 41165*, 5-10 miles south-west of Cairns; L.A.C.M. 41173*, 41182*, 41193*, 41195", Yungaburra; A.M.N.H. 19939*, Vine Creek near Ravenshoe; A.M.N.H. 54176*, Maalan Sutties Gap Road, 12 miles south of Millaa Millaa; S.A.M. R.16794-8, Gadgarra S.F.; U.A.Z. A.23, D.322, Gadgarra S.F.; Q.M. J.30902*, J.32081*, J.32140*, Paluma, Mt. Spec.

Central Population: N.P.W.S. N.11819-20, Bulburin S.F.; N.P.W.S. A.882, Conway N.P.; N.P.W.S. A.914-8, Eungella N.P.; N.P.W.S. N.12295-7, N.12339-80, Eungella N.P.; Q.M. J.23847-8, Bulburin via Lowmead; S.A.M. R.16780-3, R.16828, Eungella N.P.; U.A.Z. A.22, A.25, A.27, D323-7, Eungella N.P..

Southern Population: Q.M. J.28249*, Cooyar-Maidenwell Road; Q.M. J.29009*, Upper Reaches, Bulumba Creek, Kenilworth S.F.; Q.M. J.13119*,

VARIATION IN *LITORIA CHLORIS*

Beechmont; Q.M. J.27545, J.27551, Bunya Mountains; Q.M.J.17102*, J.17105*, J.17107-8*, Mt. Nebo; Q.M. J.17103, Methodist Youth Camp, Cunningham's Gap; Q.M. J.17104, J.17106, J.17099, Dum Dum-Murwilla Road; Q.M. J.17101, Dum Dum; Q.M. J. 23692, J.23694, Mt. Glorious; N.P.W.S. A.10, Mt. Tamborine; N.P.W.S. A.478*, A.325, A.327, Warrie N.P.; N.P.W.S. A. 487, A.537, Bunya Mountains N.P.; N.P.W.S. A.576, Ravensbourne N.P.; N.P.W.S. A.586, Mt. Glorious near Maida N.P.; N.P.W.S. N.11821-2, Mudgereeba Road, near Springbrook; N.P.W.S. N.11775-7, Conondale Range, Bellthorpe S.F.; N.P.W.S. A.560-1, A.122-3, Lamington N.P.; N.P.W.S. N.17930*, N.28268*, Kilcoy Creek, Conondale Range; N.P.W.S. N.28280-2*, Murumba Creek, Jimma S.F.; S.A.M. R.16786-93, Conondale Range, Bellthorpe S.F.; S.A.M. R.16784-5, Warrie N.P., Springbrook; A.M. R.5846, Woolongbar, Richmond River; A.M. R.7339, Goangara near Walgett, N.S.W.; A.M. R.7484-7, R. 7490-1, Dunoon, Richmond River, N.S.W.; A.M. R.9902, R.25992, Gosford, N.S.W.; A.M. R.1635-6, Lowana, N.S.W.; A.M. R.35535-42, R.35544-57, Boyd River on Oakwood Fire Trail; A.M.N.H. 62909-10*, Dunoon, Richmond River; K.U. 138729*, Tumby Umbi, N.S.W.; U.A.Z. A.26, D328-33, Warrie N.P., Springbrook.

Specimens for skeletal examination were cleared and stained using Alizarin Red S following slight modification of the technique of Davis and Gore (1947). Modification included differing times in solutions, all end points being subjectively estimated. Dried skeletons were prepared by manual flensing of the majority of soft tissue, then immersing the bones in a dilute solution of sodium hypochlorite to remove the remaining tissue and bleach the bones. All skeletal material is registered in the University of Adelaide Zoology Department Collection (UAZ).

Osteological descriptions follow Trueb (1973) and morphological descriptions follow Tyler (1968). External morphological measurements were taken using dial calipers following the method of Tyler (1968). Measurements were recorded in millimetres. These were: snout to vent length (S-V); tibia length (TL); head length (HL); head width (HW); eye to naris distance (E-N); internarial span (IN); eye diameter (E); tympanum diameter (T). From these the following ratios were calculated: TL/S-V; E-N/IN; HL/HW; HL/S-V.

Data were analysed using a student t-test and results displayed graphically by the method of Simpson, Roe and Lewontin (1960) based on that of Hubbs and Hubbs (1953).

GEOGRAPHICAL DISTRIBUTION

The distribution of *Litoria chloris* is shown in Figure 1. Three disjunct areas are apparent and these have been defined as follows:

1. Northern population; that area ranging from Cooktown to Mt. Spec.
2. Central population; that area ranging from Proserpine to Bulburin.

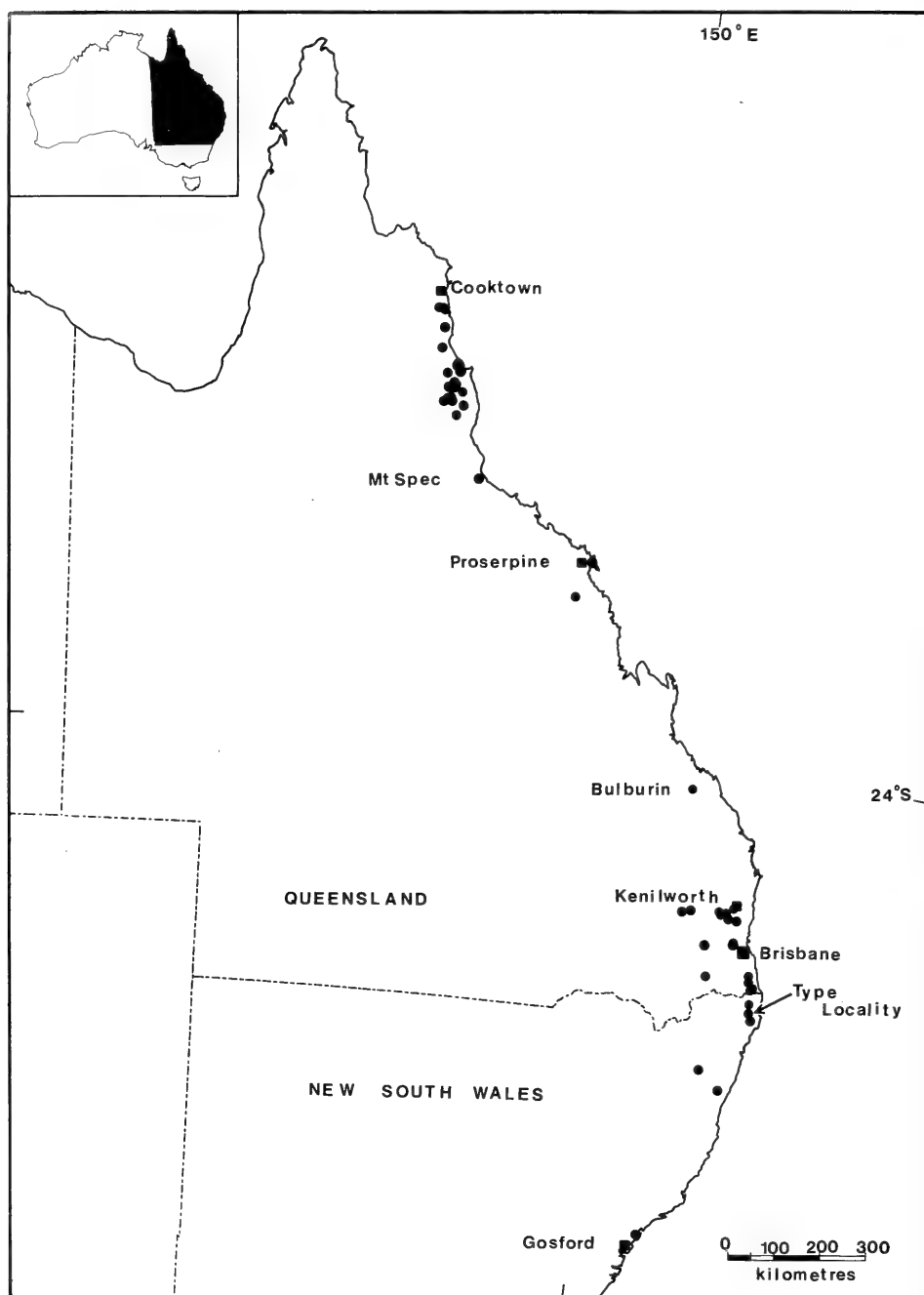


FIG. 1. Distribution of *Litoria chloris* (Boulenger).

3. Southern population; that area ranging from Kenilworth to Gosford.

The three populations will be referred to as northern, central and southern populations throughout this paper.

RESULTS

Detailed descriptions of representatives of the southern population are followed in text by comparisons with the other two geographical isolates. Morphometric measurements are expressed as mean \pm standard deviation (in mm).

EXTERNAL MORPHOLOGY

The head is slightly longer than broad (HL/HW 1.03 ± 0.03), its length equivalent to about one third of the snout to vent length (HL/S-V 0.31 ± 0.02). The snout is truncate when viewed from above, slightly rounded in profile and is not prominent. The nares are more lateral than superior, their distance from the end of the snout being less than one half that from the eye. The distance between the eye and naris is usually greater than the internarial span (E-N/IN = 1.07 ± 0.11). The canthus rostralis is slightly defined and gently rounded. The eye is large and prominent (4.75 ± 1.22), its diameter greater than the eye to naris distance. The tympanum is distinct, the tympanic diameter being slightly less than the eye diameter (3.37 ± 0.39) and separated from the eye by a distance of about $\frac{2}{3}$ of its own diameter. The vomerine teeth are in two small round groups lying close together on each side of the midline and on a level with the posterior borders of the choanae. The tongue is moderately large and oval with a slightly indented posterior edge.

The fingers are short and narrowly fringed laterally. Their order of length $3 > 4 > 2 > 1$. The webbing between the third and fourth fingers reaches the top of the subarticular tubercle at the base of the penultimate phalanx. The terminal discs are prominent.

The hind limbs are moderately long and slender (TL/S-V 0.53 ± 0.02). Toes in order of length are $4 > 3 > 5 > 2 > 1$. The webbing of all toes except the fourth reaches the base of the discs. On the fourth toe, the webbing extends to a point slightly above the subarticular tubercle at the base of the penultimate phalanx. There is a small oval inner metatarsal tubercle and a scarcely detectable oval outer metatarsal tubercle.

The dorsal and lateral surfaces of the head and body are finely granular. Prominent plicae are present on the posterior surfaces of the forearm and tarsus. There is a prominent and slightly curved supratympanic fold extending from the eye to a point adjacent to the insertion of the forearm. The throat, chest and abdomen are granular and the lower surface of the thighs tubercular.

In the male, the nuptial pad of the first finger is glandular extending to the base of the disc. A submandibular vocal sac is present.

Colour in preservative: The dorsal surface of the head, body, forelimbs, fourth finger, tibia, posterior edge of tarsus, and dorsal surfaces of fourth and fifth toes are pale blue. The dorsal and posterior surfaces of the thighs are mauve to deep violet. The plicae on the forearm and tarsus are white.

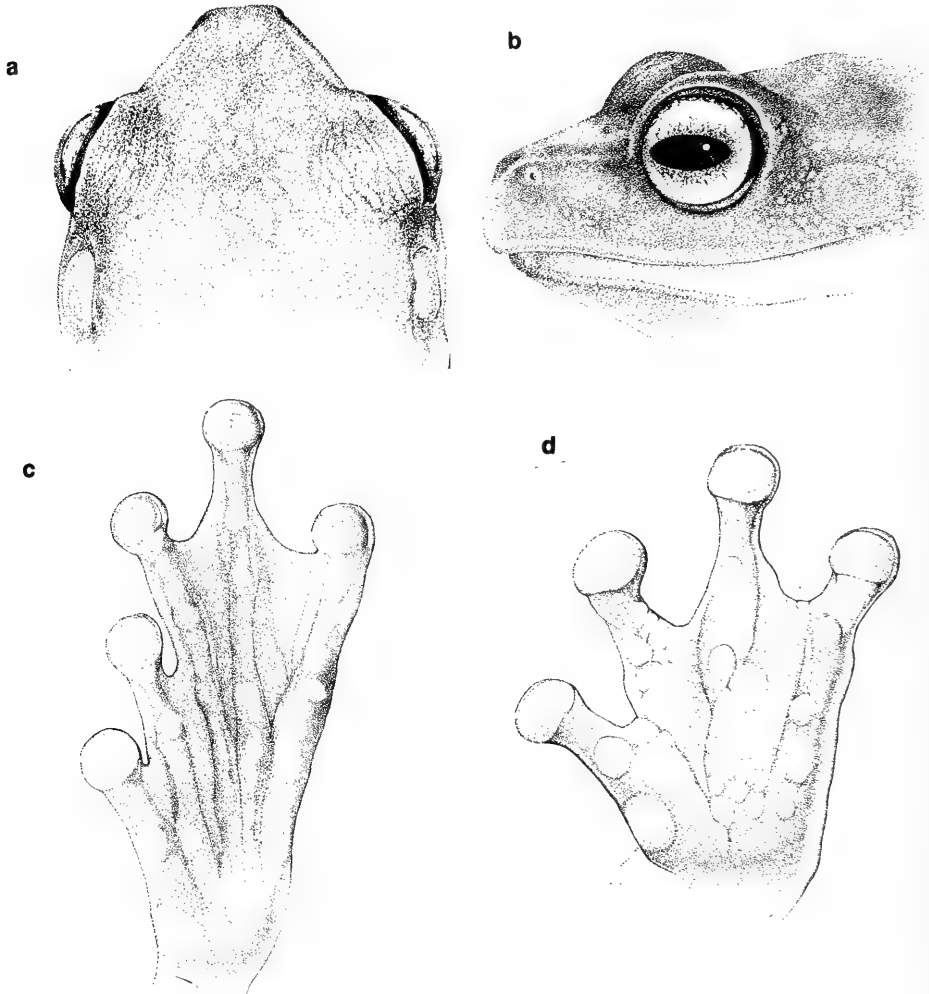


FIG. 2. a) Dorsal and b) lateral view of head, c) foot, and d) hand of *Litoria chloris*, SAM R.16828, from Eungella National Park, Qld (central population).

VARIATION IN LITORIA CHLORIS

Colour in life: Those portions of the frog that are pale blue in preservative are a brilliant lime in life. Thigh colour ranges from bluish mauve to purple. The iris is peripherally a deep orange to red with a pale border surrounding the pupil. In males the submandibular region is a brilliant yellow.

VARIATION BETWEEN THE THREE POPULATIONS

Morphological variation between the three populations is shown in Figure 3.

The head is longer than broad in both the central (HL/HW 1.03 ± 0.03) and northern populations (HL/HW 1.06 ± 0.03). The head length/head width ratio of the northern population is significantly different from that of the other two populations. The head length/snout-vent lengths in all populations are approximately equal (HL/S-V = 0.32 ± 0.02 in both central and northern populations). Head and snout shape do not vary between frogs from different localities (Fig. 2). In all cases the distance from the eye to naris is greater than the internarial span (E-N/IN = 1.04 ± 0.10 in the central population and 1.11 ± 0.15 in the northern population). E-N/IN in the northern population differs significantly from the control population but not from the southern population. The eye is large and prominent in all specimens (4.63 ± 0.40 — central, and 4.95 ± 0.51 — northern), its diameter always being greater than the eye to naris distance. The tympanum diameter is less than the eye diameter in all specimens (2.99 ± 0.28 in central frogs and 3.05 ± 0.41 in northern frogs).

Position of the vomerine teeth does not vary, nor does the general shape of the tongue. Webbing, finger and toe lengths and size of discs do not vary between populations (Fig. 2). There is little to no variation between relative tibia and snout-vent lengths in all three populations (TL/S-V = 0.54 ± 0.03 in both central and northern populations), yet both snout-vent lengths and tibial lengths are significantly different between all three populations. Frogs from the southern population are larger than frogs from the northern one and the latter are larger than those from the central population.

Body colouration varies little between the three populations with the exception of the absence of a narrow green streak running along the dorsal surface of the thighs in frogs from the central population and the considerable variation in thigh colour between the three groups. In comparison with the thighs of southern frogs, the colour of the thighs of central frogs is more intense, being a deep blue in life and purple in preservative whilst the thighs of northern *L. chloris* are bright orange in life, and colourless in preservative. Variation in iris colour is also apparent, being a golden orange in northern frogs as opposed to the more reddish tint of the other two groups.

CRANIAL OSTEOLOGY

Dorsal, ventral and lateral views of the skull of *Litoria chloris* (U.A.Z. D329 — southern population) are shown in Figure 4. The skull is moderately well

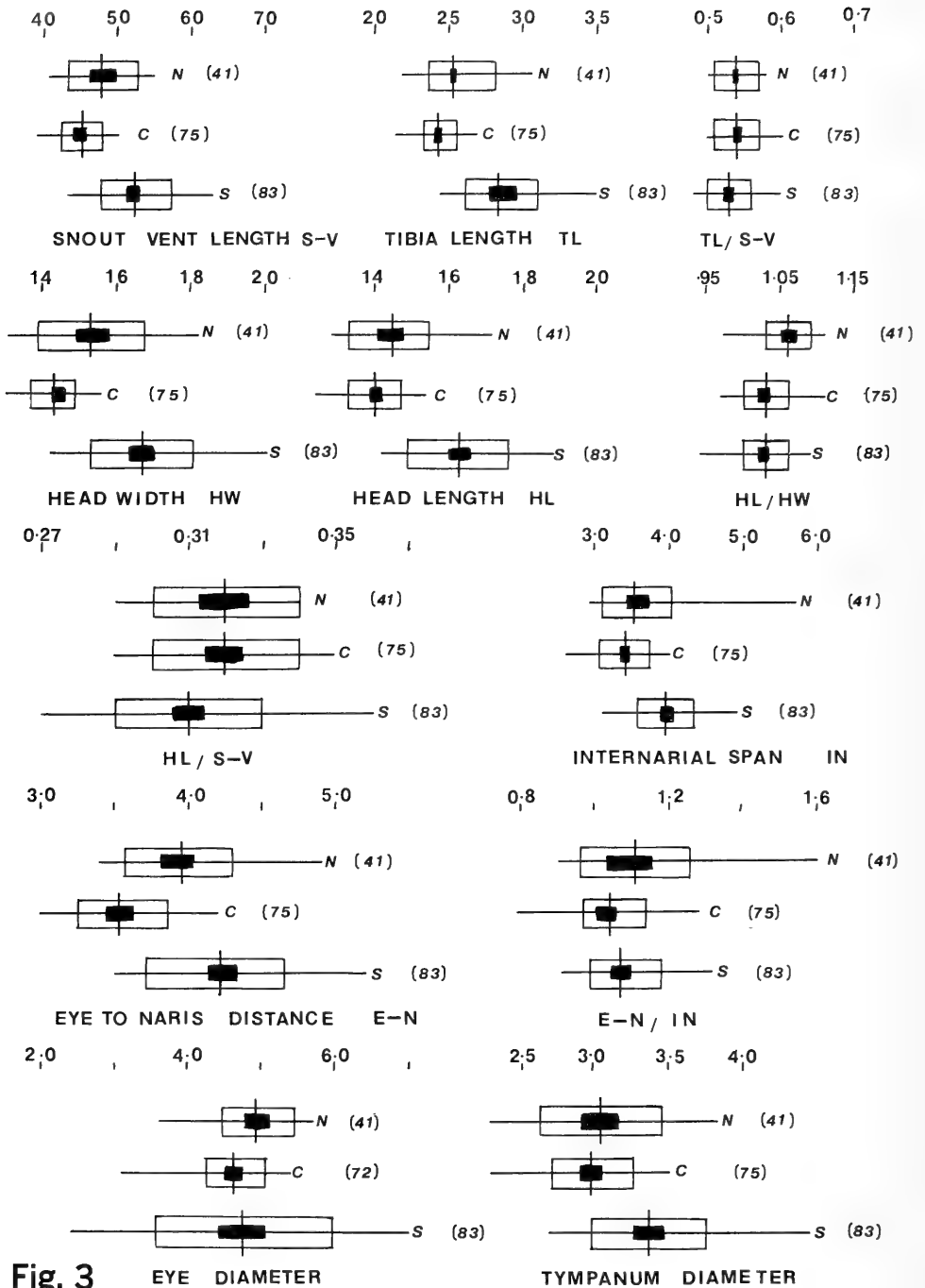


Fig. 3

ossified and slightly broader than it is long. A large portion of the sphenethmoid is ossified to lie between the nasals dorsally and the prevomers ventrally. The prootic and exoccipital regions are completely fused. The crista parotica are well developed, moderately narrow laterally with prominent epiotic eminences. The otic rami of the squamosals lie alongside the lateral extremities of the crista parotica. The zygomatic ramus of the squamosal is slightly longer than the otic ramus and extends one third of the distance to the maxillary. The frontoparietal fontanelle is moderately sized and is ovoid, the anterior margin being formed by the sphenethmoid about one third posteriorly along the length of the orbit; the posterior margin is approximately level with the posterior edge of the orbit. The orbital edges of the frontoparietals are straight and there are no crests or flanges.

The nasals are moderately narrow bones with acuminate maxillary processes making contact with the preorbital process of the pars facialis of the maxillary. The nasals overlap the sphenethmoid along their posterior edges. The palatines are long and slender medially, not ridged and are expanded laterally to lie alongside the maxillary. The parasphenoid is robust, the cultriform process being acuminate and extending for $\frac{2}{3}$ of the length of the orbit. The alae are moderately narrow, of moderate length and directed slightly posterolaterally. The pterygoid is well developed, the short medial arm not being in bony contact with the prootic region and the anterior arm stretching for approximately $\frac{2}{3}$ of the length of the orbit.

The quadratojugal is slender and in firm contact with the maxillary. The squamosals are moderately robust with a slightly expanded otic plate. A bony columella is present. The maxillaries and premaxillaries are dentate. The pars facialis of the maxillary is deep with a moderately developed preorbital process. The alary processes of the premaxillaries are moderately separated medially, expanded dorsally and slightly inclined posteriorly. The palatine processes of the premaxillaries are moderately well developed and meet at their extremities. The palatal shelf is moderately narrow with a moderately developed pterygoid process. The prevomers are entire with short dentigerous processes. The alae of the prevomers form the anteromedial margins of the choanae.

APPENDICULAR SKELETON

There are eight procoelous, non-imbricate presacral vertebrae. The sacral diapophyses are moderately expanded and the ilia extend anteriorly to them.

FIG. 3. Morphological variation in three populations of *Litoria chloris*. The short vertical line is the sample mean and the horizontal line is the range of variation. The black bar represents the 95% confidence limits on each side of the mean and the open bar indicates one standard deviation of the mean. The number of observations is indicated in parentheses. A significant difference between samples is indicated by non overlap of the black bars. N = Northern Population; C = Central Population; S = Southern Population.

Sacrococcygeal articulation is bicondylar. The relative lengths of the transverse processes of the presacral vertebrae are: Sacrum > III > IV > V = VI = VII > VIII > II.

The arciferal pectoral girdle is robust and both prezonal and postzonal elements are present. The coracoids are well developed and not closely juxtaposed and the clavicles are slender and strongly arched.

The intercalary structures are not ossified and there is no flange present on the third metacarpal. The phalangeal formulae are 2, 2, 3, 3;; 2, 2, 3, 4, 3.

VARIATION

Variation in cranial characters between the three populations is minimal but that observed such as the distribution of ossification of the sphenethmoid and nasals may be attributed to ontogenetic effects. The alae of the parasphenoid appeared slightly longer in both central and northern populations than in southern frogs, but quantification is difficult.

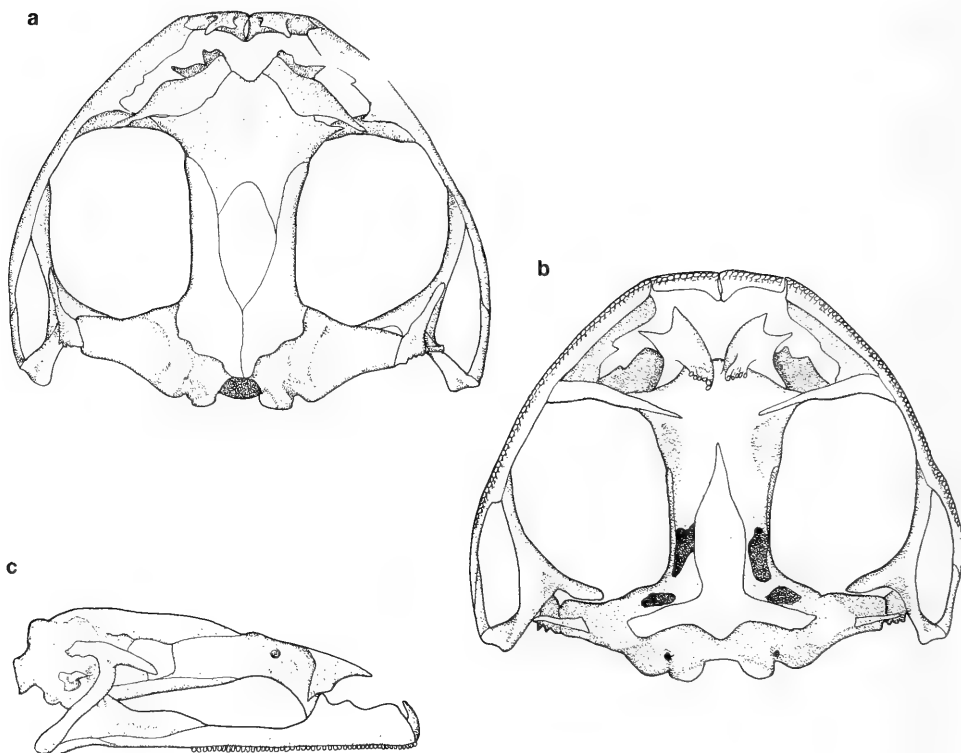


FIG. 4. a) Dorsal, b) ventral, and c) lateral views of the skull of *Litoria chloris* (UAZ D329) — Springbrook National Park, Qld (southern population).

VARIATION IN LITORIA CHLORIS

Variation was apparent in the relative lengths of the transverse processes of the presacral vertebrae. In central frogs $\text{III} > \text{Sacrum} > \text{IV} > \text{V} = \text{II} = \text{VI} = \text{VII} = \text{VIII}$ whilst in northern frogs $\text{III} > \text{Sacrum} > \text{IV} > \text{VI} = \text{VII} = \text{VIII} > \text{V} > \text{II}$.

Sacral diapophyses expansion and relative ilia position together with other appendicular skeletal characters recorded for southern populations showed little or no variation in all groups.

HABITAT

Litoria chloris occurs high in the trees in a wide range of closed forest habitats, at altitudes ranging from 5-950 m above sea level. Frogs have been collected in Araucarian microphyll vine forest, notophyll and mesophyll vine forests and sclerophyll vine forest (nomenclature of Webb, 1959). No preference for a particular forest type is apparent. It is rarely encountered except during the breeding season when individuals descend to the ground and can be found at suitable pools within the forest or in adjacent areas.

BREEDING BIOLOGY

In Queensland breeding occurs between October and March with a peak of activity from November to February. Spasmodic calling may be heard as early as September if rain falls. Heavy rainfall is a prerequisite for breeding as in *L. gracilentia* and *L. caerulea* (K.R.M., unpublished data).

Large congregations of calling males form around static pools at the edge of streams, and semi-permanent or ephemeral water bodies including road drains, water tanks and flooded quarries. The size of the breeding congregation may be influenced by the rainfall; in the Bunya Mountains, Queensland, in January 1974 more than 220 males were found calling along a 10 x 1 m roadside gutter transect during cyclonic rain.

The call is a growl lasting about 1 second which is repeated many times at increasing intensity. The last growl in a sequence is followed by two or three short trills. We were unable to detect differences by ear in call structures between males of the three populations.

Amplexus is axillary (characteristic of *Litoria*) and occurs near the breeding site; the pair then moves into the water. Spawn is deposited as a clear, flat, jelly-like mass on the surface. In shallow pools spawn has been found covering the surface whereas in pools deeper than 8 cm, it is deposited at the edges. Twelve masses of eggs from the Conondale Range had a mean of 1306 eggs in each, standard deviation of ± 228 and range 812-1561. Eggs have dark brown animal poles and separate jelly capsules. Fertile eggs sink and adhere to twigs, leaves or grass. Watson and Martin (in press) describe larval structure and life history.

Other species sharing *Litoria chloris* breeding sites include *L. gracilentia* (Peters), *L. lesueuri* (Duméril and Bibron), *L. pearsoniana* (Copland), *Lechriodus fletcheri* (Boulenger), *Adelotus brevis* (Gunther), *Mixophyes fasciolatus* Gunther, *M. iteratus* Straughan, *Rheobatrachus silus* Liem and *Taudactylus diurnus* Straughan and Lee.

DISCUSSION

The external morphology and osteology of the three geographically separated populations of *Litoria chloris* were analysed. Little or no variation in osteology was detected and variation in external morphology is limited to colour pattern and head shape. While the colour of the thighs in the central population is closely similar to that of the southern population, individuals from the north are markedly different being orange instead of deep blue or mauve to purple. The northern population further differs from the central and southern populations in the head length/head width ratio but these rather minor differences do not warrant recognising the northern population as a distinct taxon. Straughan (1966) was also unable to differentiate between the call structure of the northern and southern populations.

Faunistically each of the areas is characterized by the existence of a number of endemic species of amphibians and lizards. In the northern area, *Taudactylus acutirostris* (Anderson), *T. rheophilus* Liem and Hosmer, *Litoria nannotis* (Andersson), *Goniocephalus boydii* (Macleay), *Sphenomorphus tigrinum* (de Vis) and *Carphodactylus laevis* Gunther occur, and in the central area there are *T. eungellensis* Liem, *Phyllurus caudiannulatus* Covacevich and two undescribed *Sphenomorphus* species. Endemic species found in the southern area are *Lechriodus fletcheri* (Boulenger), *Egernia major* (Gray), *Goniocephalus spinipes* (Duméril) and *Sphenomorphus murrayi* (Boulenger).

At present it is premature to speculate about the causal factors of this high degree of speciation but, in so far as the present study is concerned, it is conceivable that the populations of *Litoria chloris* analysed here have been subjected to the same pressures, and are in the process of differentiating. However, they may have attained already unique biological integrity.

In the past, the degree of morphological variation reported here has been considered sufficient to merit the erection of new species in populations studied in the southeast and southwest of Australia (e.g. Copland 1957). However, in the absence of supporting biological data such as mating calls and comparative larval morphology, we consider it would be premature at this stage to recognise separate taxa.

VARIATION IN LITORIA CHLORIS

ACKNOWLEDGEMENTS

This manuscript was critically read by M. J. Tyler and A. A. Martin and their valuable comments are gratefully appreciated. Figure 1 is the work of Mr. T. Luck and Figure 2 of Miss K. Bowshall. The loan of material from the Australian Museum, the Queensland Museum, the American Museum of Natural History, the University of Kansas Museum of Natural History and the Los Angeles County Museum is acknowledged and we thank the respective curators—Dr. H. G. Cogger, Mr. G. Ingram, Dr. R. G. Zweifel, Dr. W. E. Duellman and Dr. J. Wright. Assistance from Messrs. R. Atherton, V. R. J. Hansen, C. J. Limpus and other officers of the Queensland National Parks & Wildlife Service is appreciated. This project was supported by an A.R.G.C. grant to M. J. Tyler.

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Oviparity and captive breeding in the Spotted Blacksnake, *Pseudechis guttatus* (Serpentes; Elapidae)¹

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ABSTRACT

Oviparity (egg-laying) is recorded as the mode of reproduction of the Spotted Blacksnake, *Pseudechis guttatus*, in both central and southern parts of the species range. Data are provided also on reproductive seasons, clutch sizes, incubation periods and hatchling sizes.

INTRODUCTION

The mode of reproduction in the large, highly venomous snakes of the Australian elapid genus *Pseudechis* has been the subject of much confusion. There is no doubt that the Red-Bellied Blacksnake (*P. porphyriacus*) bears live young, and in fact shows placental transfer of nutrients (Shine 1977). The Mulga Snake (*P. australis*) has been regarded as live-bearing also (McPhee 1959, Worrell 1963), although Gow (1976) noted an unconfirmed report of oviparity (egg-laying). The Spotted Blacksnake (*P. guttatus*) usually has been regarded as live-bearing (McPhee 1959, Worrell 1963; Kinghorn 1964). McPhee's (1959) record is particularly interesting, since he noted that a captive specimen "laid eight immature fertile eggs", but interpreted this as ovoviviparity (live-bearing). McPhee later (1979) reinterpreted this record as oviparity. Gow (1976) suggested that *P. guttatus* is egg-laying, but provided no specific data. The present report confirms oviparity as the mode of reproduction in captive *P. guttatus*.

P. guttatus is a large diurnal snake distributed through southeastern Queensland and northeastern New South Wales (Cogger 1979). Captive breeding records were obtained from snakes collected from both central and southern parts of the species' range (Fig. 1).

METHODS AND RESULTS

(1) *Queensland breeding record*

Both male and female snakes are of the dark ("Blue-Bellied Blacksnake")

(1) Please send reprint requests to Shine.



FIG. 1. Geographic distribution of the Spotted Blacksnake, *Pseudechis guttatus* (diagonal lines), showing location of specimens discussed in text (dots).

colour phase. The female is currently (April 1979) of snout-vent length (SVL) 90 cm, and weight 350 gm. She was collected in October 1976 from Oakey, Qld. (near Toowoomba). The male (current SVL = 91 cm, weight = 560 gm) was collected from Meandarra, Qld. (near Goondiwindi). Both snakes were maintained in Brisbane, and successful reproduction occurred in 1977 and in 1978. In 1977, the female laid 7 eggs on 16th December; 5 of these hatched after 12 weeks incubation at room temperature. In 1978, mating was observed in early December, and 10 eggs were laid on 26th December. One egg failed to develop, but the others were incubated successfully. Five eggs kept at a constant 24°C hatched after 12 weeks. The other 4 were maintained at room temperature, and hatched in 11 weeks.

Neonates were light silvery grey in colour, with black spotting and dark heads. Two specimens measured on 12 April 1979 (two weeks after hatching) had SVL's of 22.6 and 24.2 cm. Eggshells and hatchlings from both years' reproductions were deposited in the Queensland Museum (1977 breeding — eggshells J32036, hatchlings J32035; 1978 breeding — eggshells J35645, hatchlings J35570 and 35571).



FIG. 2. Hatching of *Pseudechis guttatus*. Upper = egg after initial incisions by young snake; lower = snake in process of hatching.

(2) *New South Wales breeding record*

The female snake (again, of "Blue-Bellied Blacksnake" colour phase) was collected from 20 km west of Dubbo, N.S.W., on 8 October 1977. This snake was 1.05 m in total length, and was kept in Sydney. She laid 13 eggs on 19 December 1977: two eggs died, but the other 11 were successfully incubated at 29°C. Hatching commenced on 14 February, but most neonates remained inside the shells for a further 24 hours (Fig. 2). The young snakes were silver-grey in colour, similar to the Queensland hatchlings described above. Mean total length of the 11 hatchlings was 28.1 cm (range 27.0 — 29.0 cm). The young snakes fed readily on small scincid lizards. Three of the snakes were deposited in the Australian Museum soon after hatching (numbers R77371-77373).

DISCUSSION

The Queensland and New South Wales records agree in several important respects: oviparity, dates of egg-laying, hatchling sizes, hatchling colouration and incubation period. Hence, there is unlikely to be marked geographic variation in these reproductive characteristics of *P. guttatus*. Nonetheless, we conclude this paper with an anomalous observation. One of us (N.C.) has seen an adult brown-phase *P. guttatus* under a log together with newly-born young in the field (near Forest Hill, 30 km E Toowoomba, Qld.), suggesting a live-bearing habit. The young were enclosed in transparent membranes similar to those that cover neonates of the related (live-bearing) *P. porphyriacus*. Cases of intraspecific variability in reproductive mode are rare (Tinkle and Gibbons 1977), so this apparent example deserves further study. Data on the other *Pseudechis* species for which mode of reproduction is doubtful — *P. australis*, *P. colletti* and *P. papuanus* — are also needed.

ACKNOWLEDGEMENTS

The authors are grateful to Jeanette Covacevich and Charles Tanner for stimulating our interest in the problem; to Greg Czechura and Judy Caughley for bringing us together; to Terry Adams for providing the Queensland snakes; and last but not least, to Margaret Charles for assistance in maintenance of the specimens.

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OBITUARY



WILLIAM SOPPITT STEEL, O.B.E.

Mr. W. S. (Bill) Steel, born in Britain on March 2, 1920, passed away in Royal North Shore Hospital on August 1, 1979 after a short illness. Mr. Steel joined the National Parks and Wildlife Service in 1969 as Assistant Director (Wildlife) and served in that position until his death. In his capacity as Assistant Director (Wildlife), Mr. Steel was in charge of all wildlife management, research, resource investigation, land acquisition, wildlife licensing and law enforcement, Aboriginal and historic resource investigation and management. His responsibility also extended to promoting an understanding of the Service and its functions through publications, displays, seminars and the media.

Following service in Europe with the British Army, Mr. Steel commenced a degree in zoology at London University, graduating in 1948 with honours in zoology. He then joined the British Colonial Service and worked for twenty years in Zambia (previously Northern Rhodesia).

His first task in Zambia was to develop methods of controlling the tsetse fly which is the principal vector of the small parasite causing sleeping sickness which was widespread in the country. The work involved detailed studies of the ecology and control of tsetse fly through spraying programmes, habitat manipulation and game management. As a result of this work, the incidence of sleeping sickness was greatly reduced, and Mr. Steel was awarded the Order of the British Empire (O.B.E.).

Following the independence of Zambia, Mr. Steel became the Director of Game and Fisheries in that country. In this position, he was responsible for many innovations. These included the introduction of controlled harvesting of elephants to both reduce habitat damage and provide food and ivory for the local population, and the introduction of new stocks of fish into Lake Kariba to increase the supply of protein for the Zambian people.

For his work in Zambia, Mr. Steel was honoured by Dr Kenneth D. Kaunda, President of Zambia, by appointment as a Grand Officer of the Order of Distinguished Service (O.G.D.S.) in 1969. The award was given in absentia as Mr. Steel had moved to Australia.

His wide experience in wildlife management and conservation was of great value in the development of the N.S.W. National Parks and Wildlife Service, which he joined shortly after its establishment. The Service was faced with considerable difficulties in gaining confidence and credibility as a wildlife management and conservation authority, and it is largely due to Mr. Steel's knowledge, experience, political acumen and popularity with a wide sector of the community that the Service succeeded as well as it has.

His passing is greatly regretted by both his colleagues and his many friends throughout Australia.

The 1980 Australian Carnivorous Marsupial Symposium

The 1980 Royal Zoological Society of New South Wales Symposium on "Australian Carnivorous Marsupials" will be held at the School of Zoology in the University of New South Wales, Kensington, N.S.W., from 12 to 13 May. This Symposium will be followed by the 27th Australian Mammal Society Scientific Meeting, also to be held in the School of Zoology, U.N.S.W.

Taxonomic groups involved in the Symposium include dasyurids, thylacinids, myrmecobiids, notoryctids, and thylacoleonids. This restriction is partly artificial but necessary because of limited time. (Papers on other groups may of course be presented at the Annual General Mammal Society Meeting). All subject areas involving these animals are suitable as topics for the Symposium. Review papers in a general subject area (e.g. "Reproduction in Small Dasyurids") are particularly desirable, but all contributions are welcome. The papers presented (as well as others that may be submitted but not delivered orally at the Symposium) will be published in a special issue of the *Australian Zoologist* after normal refereeing procedures.

Papers may be presented as either poster-papers or normal (orally delivered) conference papers. Oral presentations should be no longer than 15 minutes (but may be as little as 5 minutes). To this time, 5 minutes will be added for discussion.

Added attractions will include Dr Pat Woolley's Dibbler film (a world debut), the (or rather a) Hobart Thylacine film, another Thylacine film (recently discovered and restored), the only film footage of a live *Notoryctes*, and possibly other films of Carnivorous Marsupials. Live attractions for devotees of chewed fingers will include several species of Planigale (*Planigale tenuirostris* and *P. gilesi*), Antechinuses (several plus *Antechinus godmani*), Dunnarts, *Dasyurus maculatus*, and live Ningauis from the Northern Territory (courtesy Dr Ken Johnson).

Participants should decide on their preference for type of accommodation as soon as possible (i.e. hotel, dormitory, private or whatever).

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The Australian National Scientific and Technological Library (ANSTEL), a branch of the National Library of Australia, has been established to improve the access of the Australian community to the world's scientific and technological literature. To this end, ANSTEL has developed a wide range of services based on computerized information retrieval systems.

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1979

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AUSTRALIAN ZOOLOGIST

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Re-Description of the Jervis Bay Tree Frog *Litoria jervisiensis* ((Anura: Hylidae), with notes on the identity of Krefft's Frog (*Litoria krefftii*))

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ABSTRACT

The holotype of *Litoria jervisiensis* (Duméril and Bibron) was examined in order to re-establish the identity of this species. *L. jervisiensis sensu stricto* (Duméril and Bibron) is a *Litoria ewingi*-like frog that occurs along the coastal fringes of New South Wales and is unusual in that it is a winter breeding species. The specific name of *jervisiensis* has been misapplied in the literature to refer to a hitherto undescribed species of *Litoria*, and which is not *ewingi*-like.

The holotype of *Litoria krefftii* Günther was also examined. The authors regard this specimen as being an unusually large example of *L. jervisiensis sensu stricto*.

INTRODUCTION

Re-description of *Litoria jervisiensis* (Duméril and Bibron, 1841) is desirable in view of the current and past uncertainty regarding its status. The common name, the Jervis Bay Tree Frog, has been used in the literature to refer to a hitherto undescribed *Litoria*, and the specific name of *jervisiensis* is often mistakenly applied to this species. Barker and Grigg (1978) follow this usage of the common name in their interpretation of the species. The undescribed species will be referred to throughout this paper as the 'Heath Frog'. As further evidence of the uncertainty of the nature of *L. jervisiensis*, Cogger (1975, see fig. 295) includes a photograph of *jervisiensis sensu stricto* (Duméril and Bibron) and identifies it as *L. ewingi*. Martin and Littlejohn (1966) present information on the breeding biology of a species of frog which they refer to as *L. jervisiensis* but which in fact is the 'Heath Frog'.

Thus the identity of *Litoria jervisiensis* has become confused with time. Clarification of this species, as well as that of the Heath Frog can only be made

after a re-examination of the holotype of *L. jervisiensis*. A description of the Heath Frog is currently being prepared by the authors.

The holotype of *Litoria krefftii* (Günther) has also been examined because of repeated speculation (e.g. by Loveridge 1935, Moore 1961) about the validity of this species and its relationship with *L. jervisiensis*.

MATERIALS AND METHODS

Specimen material was provided by the following institutions which are abbreviated below: AM Australian Museum, Sydney; QM Queensland Museum, Brisbane; ANWC Australian National Wildlife Collection, Canberra; CCAE Canberra College of Advanced Education, Canberra; and NMV National Museum of Victoria, Melbourne.

Measurements of all specimens were recorded to the nearest 0.1 mm using dial calipers. The measurements taken were snout-vent length (S-V), the distance from the tip of the snout to the posterior margin of the cloacal aperture; head length (HL), the distance between the anterior tip of the snout and the posterior extremity of the tympanic annulus; head width (HW), the maximum breadth of the head; eye-naris distance (E-N), the distance between the anterior edge of the eye and the naris; internarial span (IN), distance between the nares; eye diameter (ED), the horizontal diameter of the eye; tympanum diameter (TD), the horizontal diameter of the tympanum; and tibia length (TL), the maximum length of the tibio-fibula.

Mating calls were recorded on an Akai reel to reel tape recorder (model xv). The calls were analysed using a sound spectrograph (Sona Graph 6061B, Kay Electronics Co. U.S.A.), and chart recordings were prepared on a Fernbedienung Chart Recorder Type F-NB. Wet bulb temperature readings were taken in the field at the time when sound recordings were being gathered.

In vitro crosses were made in accordance with the techniques of Watson (1977). Control (or intertaxon) crosses were made to assess the normal survival rate of fertilised eggs. Male and female *L. jervisiensis* were collected at the Caves Beach Reserve in 1969. Male Heath Frogs were collected in the same year from an area six miles south-west of Robertson in N.S.W. and male *L. verreauxi* from an area 2½ miles north-west of Nowra, N.S.W.

RESULTS

RE-DESCRIPTION OF THE HOLOTYPE OF LITORIA JERVISIENSIS

Hyla jervisiensis Duméril and Bibron 1841, *Erpét. gén.*, 8: 580. Holotype: Muséum National d'Histoire Naturelle 4826 from Jervis Bay, New South Wales.

RE-DESCRIPTION OF JERVIS BAY TREE FROG

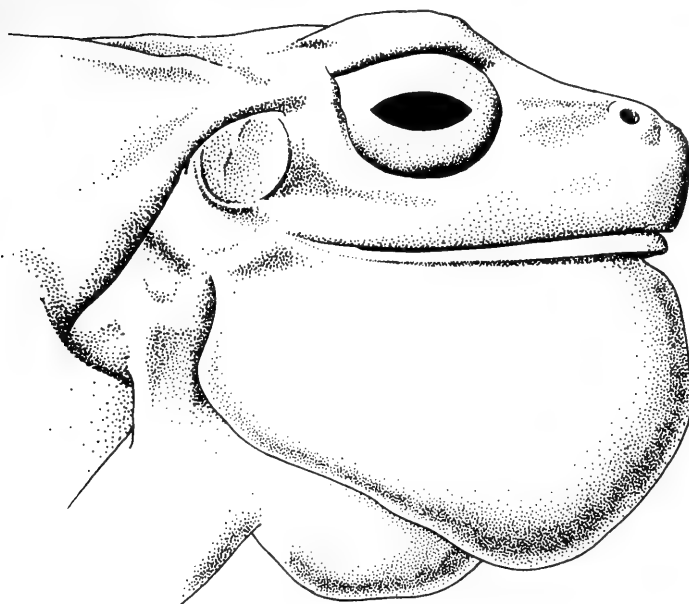


Fig. 1. Right profile of the holotype of *L. jervisiensis*.

The holotype was collected by Péron and Leseur during their travels through the southern regions of New South Wales. It is a medium sized frog (S-V 41.0 mm), slender body form, but with a relatively broad head (HL:HW 0.984). The head accounts for about one third of the total body length (HL:S-V 0.375). The snout is rounded in both dorsal and lateral aspects and projects very slightly beyond the line of the lower jaw (Fig. 1). The distance from the eye to the naris is greater than the internarial span (E-N:IN 1.167) and gives the snout a slightly elongate appearance. The nares are positioned high on the snout and are angled outwards and upwards. The eyes do not bulge above the line of the head and as a result the head appears to be flat. Nevertheless, the eyes are large, their diameters being larger than the eye-naris distance (E-N:ED 0.761). The tympanum is much smaller and less conspicuous than the eye (TD:ED 0.434) and is separated from the eye by a distance of 1.5 mm. The canthus rostralis is distinct and appears to be slightly concave when viewed from above. There is a prominent supratympanic fold which terminates near the axilla. The angle of the jaw bears a raised glandular line that still retains some traces of white colouration.

The fingers and toes possess well-developed terminal discs, especially on the more medial digits. The discs on fingers two and three are almost twice as wide as the tip of the finger. Fingers are free of webbing and the hand bears a few well developed subarticular tubercles (Fig. 2). The fingers are, in order of length

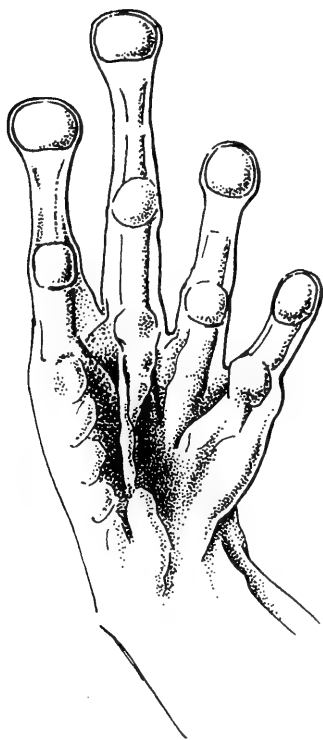


Fig. 2. Undersurface of the right hand of holotype of *L. jervisiensis*.

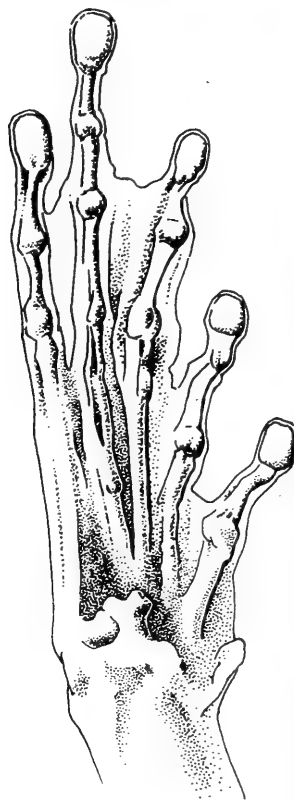


Fig. 3. Undersurface of the right foot of the holotype of *L. jervisiensis*.

4<3<1<2. Along the ventral margin of the forearm is a line of raised lumps that ends at the wrist.

The hind limbs are long and slender (TL:S-V 0.510). Webbing between the toes is extensive and reaches the discs of all the toes except the fourth where it extends as far as the base of the penultimate phalanx (Fig. 3). The toes are, in order of length, 1<2<3<5<4. There is a prominent, elongate inner metatarsal tubercle and a tiny outer metatarsal tubercle.

The vomerine teeth are small and situated in line with the anterior edges of the choanae. They are crescent-shaped and spaced well apart.

Dimensions (mm):—

External measurements: S-V 41.0 (note, this is 2 millimetres less than the original measurement taken by Duméril and Bibron); TL, 18.1; HL, 12.3; HW, 12.5; E-N, 3.5; IN, 3.0; ED, 4.6; TD, 2.0.

RE-DESCRIPTION OF JERVIS BAY TREE FROG

SPECIMENS EXAMINED

All the available specimens were collected from New South Wales. AM R27681-2, Woodford Island, Clarence R., 31.viii.1964; AM R29903, Baulkham Hills, 5.ix.1974; AM R73327, Centennial Park, Sydney, 12.vi.1978; AM R73328-33, Centennial Park, Sydney, 12.ix.1978; AM R74936, Lorne State Forest, Taree, 1.vi.1978; AM R78792-6, Smith's Lake, 30.viii.1972; AM R81666-7, Centennial Park, Sydney, 20.vi.1978; AM R81668, Mount Royal State Forest, Singleton, 22.xi.1979; QM J34222, Heathcote, —.i.1962; ANWC A0451, Batehaven, 20.i.1976; ANWC A0690, Ryan's Swamp, Caves Beach, Jervis Bay, 29.iv.1976; ANWC A1252, Ryan's Swamp, Caves Beach, Jervis Bay, 27.iv.1977; CCAE 206-11, Ryan's Swamp, Caves Beach, Jervis Bay, —.vi.1974; CCAE 216, Ryan's Swamp, Caves Beach, Jervis Bay, —.iv.1974; CCAE 265-9, Ryan's Swamp, Caves Beach, Jervis Bay, —.v.1974; NMV D6678-9, Botany Bay, pre 1877; NMV D7021, Sydney, no date.

COMPARISON WITH OTHER SPECIES

Litoria jervisiensis sensu stricto (Duméril and Bibron) is considered by the authors to be most closely related to frogs of the *Litoria ewingi* group (as referred to by Tyler and Davies 1978) and should be included within that group. This judgement is made on the basis of comparative external morphology and head shape. Table 1 lists the comparative measurements of head and body proportions of three species from the *L. ewingi* group and the Heath Frog.

The Heath Frog is not closely related to frogs of the *L. ewingi* group and can be quickly separated from these frogs on the basis of head shape. Frogs from the *L. ewingi* group have heads that are longer than they are broad. The Heath Frog has a head that is broader than it is long.

COLOURATION OF LIVE SPECIMENS

Most specimens are known from areas adjacent to Sydney, N.S.W. and therefore may not be completely representative of the colour patterns throughout the range of the species. The only noted difference in colouration between the Sydney specimens and other specimens is that the former have an intense yellow patch around the axilla (Plate 1a). Generally, the dorsal surface is smooth and two-toned brown in colour. The darker brown forms a broad, unbroken, vertebral band which becomes indistinct towards the posterior of the animal. The intensity of this band is variable and is sometimes difficult to discern from the rest of the dorsal pattern. The limb undersurfaces and ventral surface of the body are off-white in colour. The axilla and groin are yellow in colour, whereas the posterior of the thigh has a broad orange patch (Plate 1b). There are no spots or marbling in the groin or on the flanks. The specimen from Singleton is unusual in that there was a trace of orange in the crease of the groin.

CAPTION FOR PLATE 1 A AND B OPPOSITE

Plate 1(a). Adult male *L. jervisiensis* captured in Centennial Park, Sydney. This specimen has a marked white labial stripe and yellow patches about the axilla.

Plate 1 (b). Posterior view of an adult specimen of *L. jervisiensis* showing broad oval orange patches on the hind side of the thighs. There is no distinctive dorsal pattern.

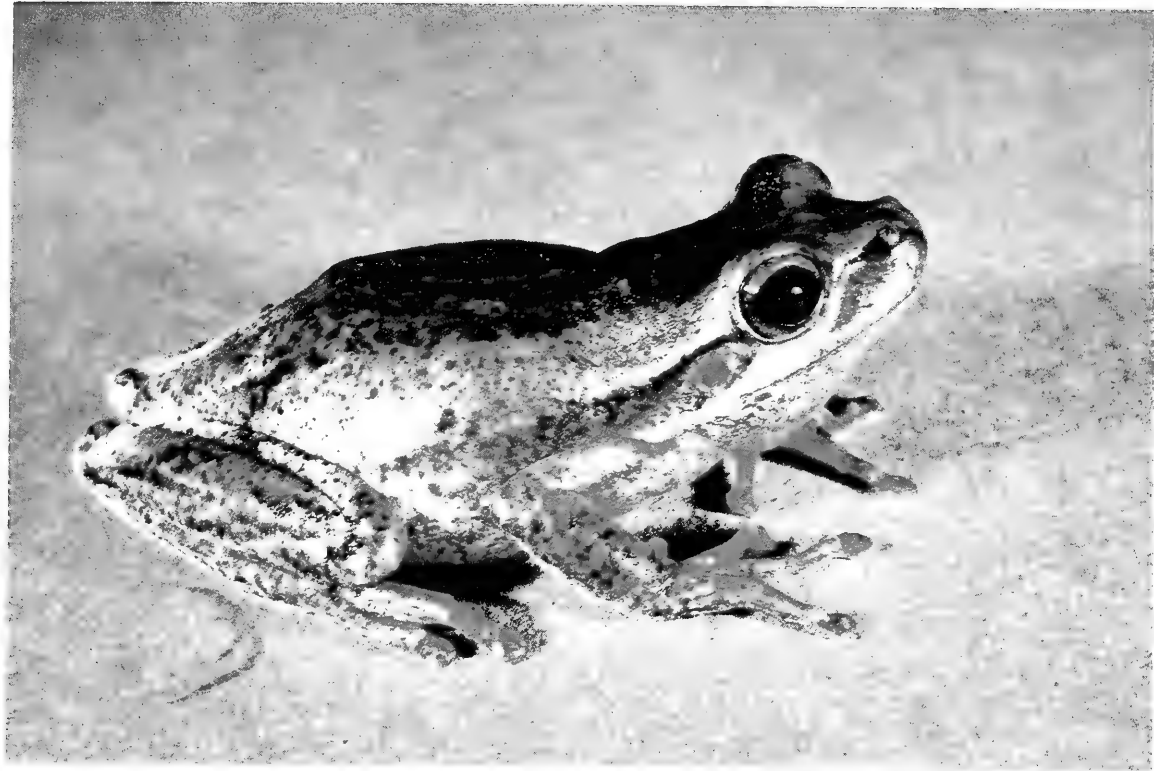


Plate 1 a & b

RE-DESCRIPTION OF JERVIS BAY TREE FROG

There is a faint white stripe along the upper labium, beginning in front of the eye, running beneath the tympanum and terminating at the axilla. The canthus rostralis is edged in brown. There is an ill-defined white band along the side of the head which runs from the posterior margin of the eye, above the tympanum and terminating above the axilla.

COLOURATION AFTER PRESERVATION

The dorsal brown colour fades to a monotone grey leaving no trace of any back pattern. The tympanic stripe dulls and disappears altogether. The white labial stripe is dulled but seems to remain in the region of the glandular elevation at the angle of the jaw. The yellow patches around the axilla and hind limbs fade completely. Similarly the orange patch on the posterior of the thigh disappears leaving a blank oval patch. The entire undersurface assumes a grey or off-white colour. The throat sometimes retains some dark pigmentation.

VARIATION

Adult snout-vent lengths range from 29.2-41.3 mm (see Table 1 for a comparison of the snout-vent lengths of other species within the *L. ewingi* group). From the specimens examined there did not appear to be a marked dimorphism in size between the sexes. The largest specimen that was examined was a male (ANWC A1252). All other species from the *L. ewingi* group show a distinct dimorphism in size between the sexes. Specimens AM R73327, AM R73328, AM R74936, AM R78792-5 and QM J34222 have nuptial pads. No gravid females were examined.

DISTRIBUTION

The localities so far investigated indicate that the species is confined strictly to coastal N.S.W. Specimens are known from Ballina, in the north, to Twofold Bay in the south. A solitary specimen from the Hunter Valley, near Singleton in N.S.W. is the most inland example collected to date. This is also the highest altitudinal record. As already indicated this specimen was slightly different in its markings. Fig. 4 shows the sites of capture of *L. jervisiensis*. Specimens from

TABLE 1

Adult Body Length Measurements and Proportions of Five Species of Frogs.

Species	S-V	TL:S-V	HL:HW	HL:S-V	HW:S-V	IN:E-N	IN:HW	ED:TD
<i>L. krefftii</i>	43.6	0.51	1.02	0.30	0.29	0.97	0.25	1.8
Heath Frog	40.1-67.0	0.51-0.61	0.83-0.98	0.30-0.37	0.31-0.38	0.78-0.93	0.21-0.28	1.6-2.4
<i>L. jervisiensis</i>	29.2-41.3	0.44-0.54	1.01-1.09	0.29-0.35	0.28-0.33	0.85-0.96	0.24-0.28	0.9-1.7
<i>L. ewingi</i>	22.5-42.5	0.50-0.56	1.01-1.07	0.30-0.37	0.29-0.36	0.73-0.90	0.21-0.25	1.0-1.5
<i>L. v. verreauxi</i>	26.3-37.7	0.34-0.53	0.94-1.01	0.28-0.35	0.28-0.35	0.86-1.00	0.25-0.30	1.4-2.2

Jervis Bay southwards were collected by Mr. K. R. Slater of the Canberra College of Advanced Education and are verified localities. It seems most probable that the range will be extended into Victoria with further collecting, especially around Lakes Entrance. Extensions of the range northwards are less likely because of unsuitability of terrain.

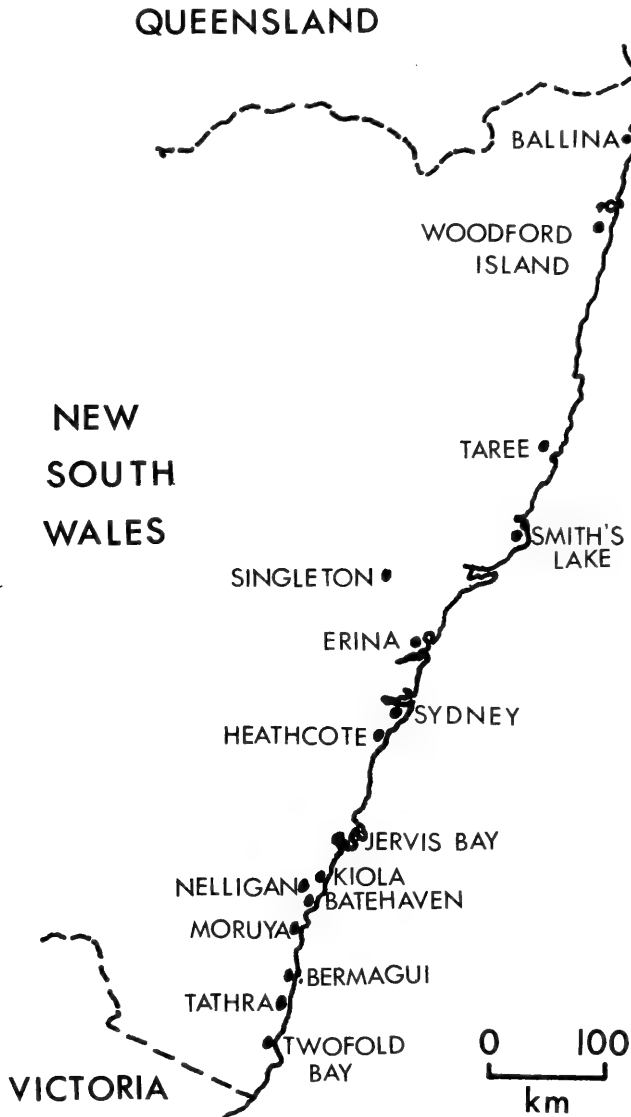


Fig. 4. Known localities of positive sightings or capture of *L. jervisiensis*.

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PREFERRED HABITAT

All specimens, with the exception of the Singleton frog, are from low altitudes. The preferred habitat seems to be still ponds, fresh water swamps or fresh water lagoons. All of these need to be of a relatively permanent nature. The critical factor at all of these sites is the presence of thick stands of emergent vegetation such as *Typha* and *Eleocharis*. In the Centennial Park system in Sydney, only one of several ponds is used by *L. jervisiensis*. This pond is away from the heavily used recreational areas of the park and as such has not been cleared. Male *L. jervisiensis* use *Eleocharis* in shallow water or *Eryngium* on the edge of the pond as calling sites. In other localities males have been observed calling from

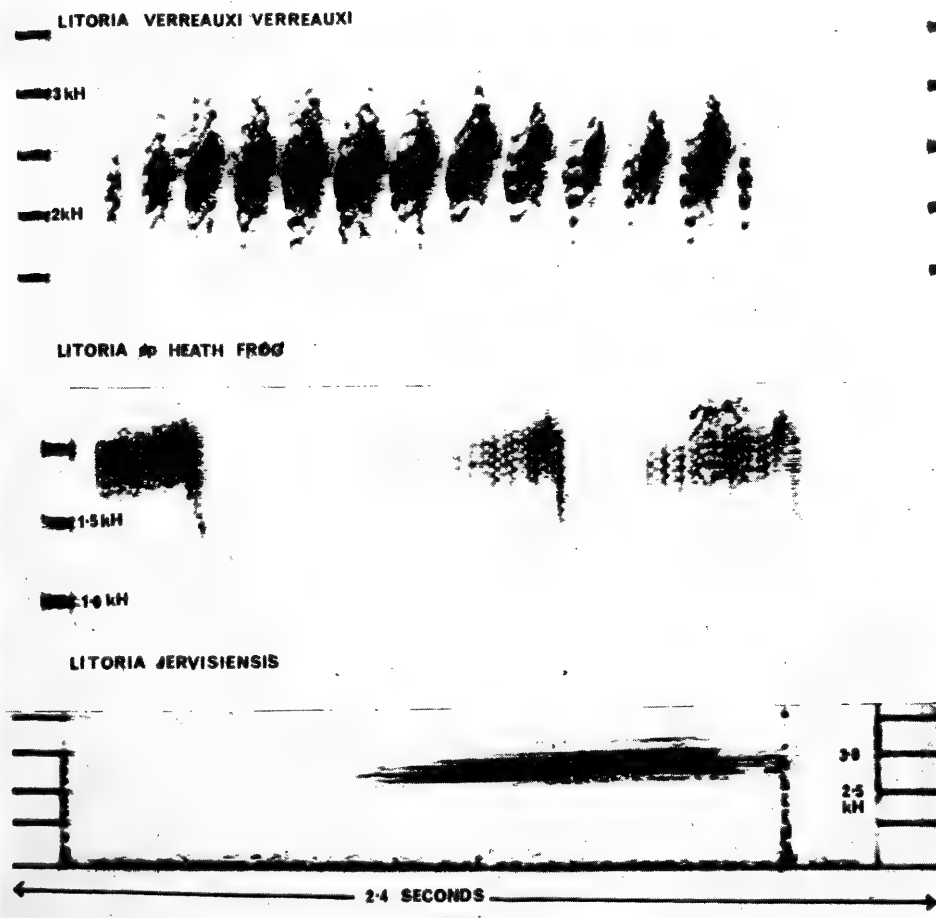


Fig. 5. Sonagram recordings of the mating calls of *L. jervisiensis*; *L. v. verreauxi* and Heath Frog.

LITORIA VERREAUXI VERREAUXI

01 02 03 04 05 06 07 08 09 10 15 20

LITORIA JERVISIENSIS

01 02 03 04 05 06 07

Fig. 6. Chart recording of the call of *L. v. verreauxi* and *L. jervisiensis*.

Typha These plants are utilised as refuge sites from predatory birds and are probably the sites for the deposition of eggs.

MATING CALL

Special attention has been placed on gaining a selection of recordings of the mating calls of *L. jervisiensis* and comparing the structure of the call with that of other closely related species that are sympatric in the Sydney area (i.e. Heath Frog and *Litoria verreauxi*). Call data for the Heath Frog is taken from Martin and Littlejohn (1966) and from the prepared recordings of Grigg and Barker (1973).

Samples of the sonagrams and chart recordings are presented in Figs. 5 and 6 respectively. Each call was analysed and the relevant data presented in Table 2.

L. jervisiensis

The mating call of *L. jervisiensis* consists generally of 2 or 3 high pitched squeals, whose frequency ranges from 1980-2831 Hz (dominant frequency 2750 Hz) and which are repeated regularly after a short (c. 20 second) interval. Both call and note duration are short, the total call lasting on an average about 2 seconds. Each note rises in intensity as each note is produced (Figs. 5 and 6).

L. verreauxi

The mating call of male *verreauxi* is unlike the other two species of frog considered. Each call is made up of 12 to 15 very short notes which tend to fuse to produce a pulsating whistle. The pitch is generally lower than that of *jervisiensis* with a dominant frequency of 2400 Hz and a range of frequencies between 1950-2800 Hz. Call duration, although made up of many notes, is short with the total call lasting about 2½ seconds.

Heath Frog

The distinctiveness of the call of this frog (and the above two species) reinforces the differences between these species. The call in this case is composed of between 6 and 14 notes, each note being a low drawn out sound. The pitch ranges from 1600-2100 Hz with a dominant frequency of about 1800 Hz (table 2). The recordings made at Darkes Forest (Fig. 5) show a downwards deflection in tone at the end of each note. This has not been noted in the call of Heath Frogs from other areas.

Pulse repetition rate has been used as a discriminating factor in the differentiation of frog calls between closely related species (Loftus-Hills and Littlejohn, 1971). The pulse repetition rates of *L. jervisiensis* and *L. v. verreauxi* do overlap (Table 2) while note duration and the number of notes per call are markedly different.

BREEDING SEASONS

Sustained observations have been kept on two populations of *L. jervisiensis* close to Sydney; one at Erina, near Gosford, N.S.W. (Dankers 1977) and the

TABLE 2
Analysis of the Mating Calls of *L. v. verreuxi*, *L. jervisiensis* and the Heath Frog. Ranges given in parenthesis.

Species	Call Duration (secs.)	Notes per Call	Note Repetition Rate	Note Duration (secs.)	Pulse Repetition Rate	Dominant Frequency (Hertz)
Heath Frog Rec'd 24-viii-63; Cann R. Martin and Littlejohn (1966) Wet bulb 8°C	9.1 (6.0-12.3)	10.7 (7-14)	70.5 (68.3-73.3)	0.67 (0.64-0.70)	38.5 (37.5-39.4)	1683 (1600-1750)
Heath Frog Rec'd 21-xi-72; Darkes Forest. Grigg and Barker (1973-track 17)	7.8 (7.0-8.8)	8.0 (6-10)	63.8 (61.5-66.4)	0.62 (0.50-0.65)	—	1800 (1600-2100)
<i>L. v. verreuxi</i> Rec'd 14-ii-73; Palmdale. Grigg and Barker (1973- track 16)	2.53 (1.9-3.0)	13.3 (12-15)	315.4 (254-378)	0.07 (0.06-0.08)	112.4 (103.6-118.4)	2400 (1950-2800)
<i>L. jervisiensis</i> Rec'd 27-v-78; Centennial Park Wet bulb 10°C	2.10 (1.4-2.5)	2.3 (1-4)	85.7 (75-118)	0.70 (0.5-0.8)	119.7 (90.0-152.5)	2750 (1980-2831)

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other at Centennial Park by the authors. The Erina populations commenced calling in mid April in 1974 and continued calling until mid October. The males ceased calling in 1973 by the end of September. In Centennial Park in 1978 the pattern was the same; calling commenced in early April and continued until late October. However, for 3 weeks during the coldest part of winter (21.vi.78-18.vii.78) calling was interrupted, resuming once the air and water temperature had warmed a little. The critical temperature seemed to be at a wet bulb reading of 6°C. Below this there was no calling by the males. Wet bulb measurements were taken as these are more equatable to frog body temperature than dry bulb readings. Calling and reproductive activity was greatest in the pre-winter period.

TABLE 3

Seasonal Calling Patterns of Three Species of Tree Frogs. "+" indicates calling in that month.

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Heath Frog	+	+	+	+/-	-	-	-	-	-	-	+	+
<i>L. jervisiensis</i>	-	-	-	-/+	+	+	+	+	+	+/-	-	-
<i>L. v. verreauxi</i>	+	+	+	+	+	+	+	+	+	+	+	+

Temperature also altered the structure of the call of the male frogs. At low temperatures (6.0-7.5°C wet bulb) the call changed, the pitch was lower and the number of notes was reduced to one or two.

Elsewhere around Sydney *L. v. verreauxi* can be heard calling on occasions during every month of the year. The Heath Frog has a distinct summer peak in calling activity and does not call during the wintertime. Thus the opportunity for hybridisation between the Heath Frog and *L. jervisiensis* is restricted to a few weeks in April (Table 3). *L. v. verreauxi* has a breeding season which encompasses that of *jervisiensis* and the Heath Frog. Both *jervisiensis* and *verreauxi* occur in the same ponds at Erina but their respective calls are so distinctive that mis-identification of the mating calls by female frogs of these species is most unlikely.

CALLING BEHAVIOUR

Observations on the preferred sites for calling by male *verreauxi* and *jervisiensis* show some behavioural differences. *L. v. verreauxi* has not been observed calling from water but does call from sites on the ground or in trees closeby. Male *L. jervisiensis*, on the other hand, prefers to call from emergent reeds. This behaviour has been noted by others (e.g. K. R. Slater; pers. comm.). The Heath Frog is less specific in its choice of calling sites and has been heard calling from low bushes, under ferns and in shallow pools. These differences in calling behaviour between the males of the three species serve to spatially separate the calling frogs according to their species.

HYBRIDISATION TRIALS

In vitro cross-fertilisation studies were carried out to assess the innate compatibility of the three above mentioned species. Ova from female *L. v. verreauxi* and female Heath Frogs were not available when these trials were conducted. The crosses that were carried out are presented in Table 4.

TABLE 4

Cross-fertilisation trials between *L. jervisiensis*, *L. v. verreauxi* and the Heath Frog.

Male	Female	No. eggs	No. fertilised	% Hatched	% Abnormal
<i>jervisiensis</i>	<i>jervisiensis</i>	86	80	90	10 ^a
Heath Frog	<i>jervisiensis</i>	40	40	0	100 ^a
<i>verreauxi</i>	<i>jervisiensis</i>	34	34	0	79 ^a , 21 ^b

a Failed to develop beyond neurulation

b Failed to hatch

The information from these crosses demonstrates that hybrids cannot occur between female *L. jervisiensis* and male Heath Frogs or male *L. v. verreauxi*. The reverse may not be true. Clearly genetic barriers do exist between *L. jervisiensis* and the other two species and these barriers serve to reinforce confidence in *L. jervisiensis* as a biological species.

KEY TO EWINGI GROUP AND THE HEATH FROG

This key is offered as a field guide and as such uses external anatomy and colouration of live specimens as discriminating characters.

1. Black spots or marbling in the groin *L. v. verreauxi*
No spots or marbling in the groin 2
2. White glandular stripe below the eye, always most prominent at the angle of the jaw 3
No white glandular stripe below the eye, axilla and posterior of the thigh bright orange Heath Frog
3. Axilla yellow, posterior of the thigh orange. Discs of the medial digits very much wider than the tip of the digit *L. jervisiensis*
Axilla not brighter than the ventral colour, posterior of the thigh either yellow or orange. Discs on the medial digits as wide or slightly wider than the tips of the digit 4
4. Canthus rostralis straight when viewed from above *L. paraewingi*
Canthus rostralis concave when viewed from above *L. ewingi*

RE-DESCRIPTION OF JERVIS BAY TREE FROG

NOTES ON THE IDENTITY OF KREFFT'S FROG

Hyla krefftii Gunther 1863, Ann. Mag. Nat. Hist. 11:28 Holotype: British Museum of Natural History 1947: 2.22.78, from Sydney, New South Wales.

The holotype was described 22 years after the naming of the *L. jervisiensis* type. Superficially it strongly resembled the *jervisiensis* type and has prompted speculation in the literature as to its specific identity. Loveridge (1935) argued that *krefftii* was a synonym of *jervisiensis*. His argument was based on the known distribution of *jervisiensis* and the fact that intensive investigation of the frog fauna around Sydney had failed to produce another individual that was similar to *krefftii*.

Copland (1957) noted the findings of Loveridge but did not appreciate that the frogs he had listed as *jervisiensis* were in fact a different species. Consequently he believed that *krefftii* and *jervisiensis* were different species. Moore (1961) used Copland's *jervisiensis* specimens as examples of that species, but also included specimens from the American Museum collection in his description of the species. Some of these specimens (Nos. 64029-64032) are *jervisiensis sensu stricto*. Moore did not query these or his other specimens but did include measurements from these frogs which showed that they were unlike the other specimens that he had included in *jervisiensis*. He furthermore presented measurements for both *jervisiensis* and *krefftii* types which reinforced the similarity between these frogs. He may have realised that there was an inconsistency in the taxonomy of these frogs but did not resolve these discrepancies.

The present authors have re-examined both type specimens. The *krefftii* type is a relatively large frog, larger in fact than the maximum recorded size for *L. jervisiensis* (Table 1). It is easily recognised by the presence of broad discs on the medial digits and relatively long tibia (TL:S-V 0.48). The fingers are free of webbing whereas the toes are extensively webbed, with all but the fourth toe being fully webbed. There is a glandular elevation at the angle of the jaw which still retains a trace of white pigmentation. The dorsal surface shows some evidence of a broad dorsal band but this has faded considerably. The vomerine teeth lie between the choanae.

On morphometric data the authors are impelled to agree with Loveridge, 1935 that *krefftii* is a synonym of *jervisiensis*. On the basis of HL:HW measurements (Table 1) *krefftii* is very similar to all of the other *ewingi* like frogs studied. On the basis of IN:E-N *krefftii* can be separated from all but *jervisiensis*. In fact the only character which might cast any doubt on its identity is its unusually large size.

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The Food and Feeding Habits of the Rock Blackfish, *Girella elevata* Macleay (Pisces: Girellidae), from the Sydney Region, New South Wales

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ABSTRACT

The stomach contents of 227 rock blackfish (*Girella elevata*), represented by adults (240-490 mm SL (Standard length)), juveniles (73-134 mm SL) and small juveniles (13-55 mm SL) collected from the Sydney region, were analysed. All three size classes of *G. elevata* examined were found to be omnivorous. Algae comprised the principal food, making up 77% of the diet in adults, 74% in juveniles and 40% in small juveniles. Small juveniles also consumed large quantities of crustaceans (36%) and the amount of animal material in their diet was significantly greater than that in the juvenile and adult size classes. These differences were correlated with growth-related changes observed in relative gut length, the alimentary tract of adult *G. elevata* being long and coiled and of a generalised herbivorous pattern.

INTRODUCTION

Girella elevata, commonly known as the rock blackfish or black drummer, has been recorded along the eastern Australian coastline from far southern Queensland to northern Tasmania (including eastern Victoria), and is also known from Lord Howe Island (Allen *et al.*, 1976). Adult rock blackfish may reach weights of approximately 8 kg and inhabit holes and crevices in shallow marine subtidal rocky reef areas. Juvenile fish occupy intertidal rock pools and shallow sub-littoral areas and small juveniles appear to be restricted to tidal rock pools within the upper littoral zone (pers. obs. authors).

G. elevata is taken by anglers and spearfishermen in limited numbers and occurs sympatrically with three other congeneric species, *G. tricuspidata* (throughout its range), *G. cyanea* (in the northern part of its range) and *G. zebra* (in the southern part of its range).

Published information on the diets of the girellid fishes is meagre. Mitchell (1953), Williams and Williams (1955) and Norris (1963) described the feeding habits of various size classes of the Californian opaleye *G. nigricans*. Thomson (1959), Russell (1971) and Kilner and Akroyd (1978) described the diets of adult *G. tricuspidata* from Australia and New Zealand and concluded that this species was generally herbivorous. Various aspects of the alimentary tract morphology of the Japanese species *G. punctata* and the American species *G. nigricans* have been described by Suyehiro (1942) and Norris and Prescott (1959), respectively. In general, most members of the family Girellidae appear to consume large quantities of plant material.

The only available information on the diet of *G. elevata* is that recorded by Stead (1908) who noted that it "subsists on gelatinous weeds", and by Roughley (1951) who recorded it as being "a weed eating fish which also takes a variety of animal fishing baits."

This study aims at determining the diet of adult *G. elevata* and assessing whether there are differences between the diets of small juvenile, juvenile and adult size classes.

MATERIALS AND METHODS

Data and biological samples from specimens of adult *G. elevata* were collected at monthly spearfishing competitions held in the Sydney region between 1 August 1976 and 6 July 1977. Fish were taken by spearfishermen from inshore rocky reef habitats between Avoca Beach ($151^{\circ}28'E$, $33^{\circ}30'S$) in the north and Wollongong ($150^{\circ}53'E$, $34^{\circ}26'S$) in the south, as described by Bell (1979). After a competitor had weighed in his fish it was measured (to the nearest mm SL (standard length)) and its alimentary tract was removed and preserved in 10% (V/V) formalin (i.e. 4% formaldehyde in water). Ten specimens were processed at each competition, except during some months when fewer specimens were caught.

Small juvenile and juvenile specimens were collected during January-1979 at low tide from rock pools, in both the upper and lower littoral zones at Bare Island (Botany Bay) and Avalon, and from the upper littoral zone at Narrabeen, all localities in the Sydney Metropolitan Area. These specimens were collected using rotenone and dip nets and were also preserved in 10% formalin.

Diet was determined by analysing the stomach contents of each fish by an estimated volumetric method (the "points" method as used by Pollard, 1973). Food organisms were separated to the lowest taxonomic level possible using a binocular microscope. Seasonal differences in the diet of adults were assessed by comparing samples taken during spring (September-November), summer (December-February), autumn (March-May) and winter (June-August).

FOOD AND FEEDING OF ROCK BLACKFISH

The percentages of plant material in the diets of the three different size classes, viz. adults, juveniles and small juveniles, were compared. The percentage data were first transformed using an arcsin transformation and 95% confidence limits were calculated for the three size classes.

The morphology of the alimentary tract was examined in 89 adult specimens. The structure of the teeth, tongue, gill rakers, oesophagus, stomach, pyloric caeca and the main components of the intestine were noted. The relative gut lengths (RGL = total gut length/standard length in mm) of adult, juvenile and small juvenile fish were calculated following the method of Al-Hussaini (1949).

RESULTS

Three distinct size classes, i.e. adults, juveniles and small juveniles, were distinguished during this study. The length frequency distribution of adults (240-490 mm SL) collected from spearfishing competitions is shown in Fig. 1, and Fig. 2 shows the length frequency distribution of juvenile (73-134 mm SL) and small juvenile (13-55 mm SL) fishes collected from tidal rock pools.

Members of a fourth size class (sub-adults), which would fall within the size range between 135 and 239 mm SL, were observed to occur in schools of up to 50 individuals beneath large boulders and ledges in the shallow sublittoral zone (pers. obs. authors). Fish of this size, however, were not sampled during the present study as they were too small to be taken by spearfishermen and proved too difficult to sample in sufficient numbers by other techniques.

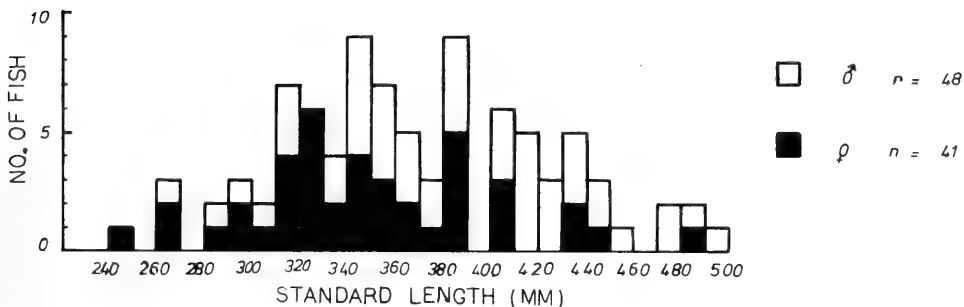


FIG. 1. Length frequency distribution in 10 mm groupings (0-9, 10-19 mm etc.) for adult *G. elevata* collected by spearfishing from sub-littoral reef habitats between 1.viii.76 and 6.vii.77.

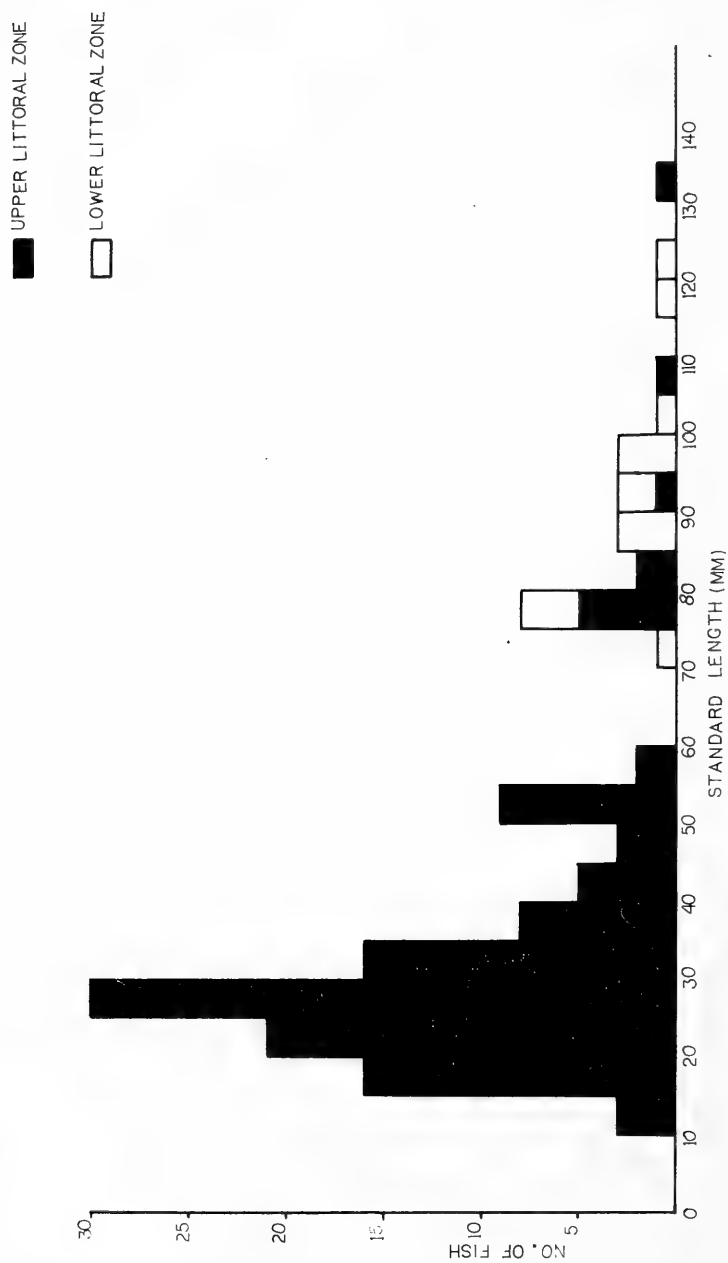


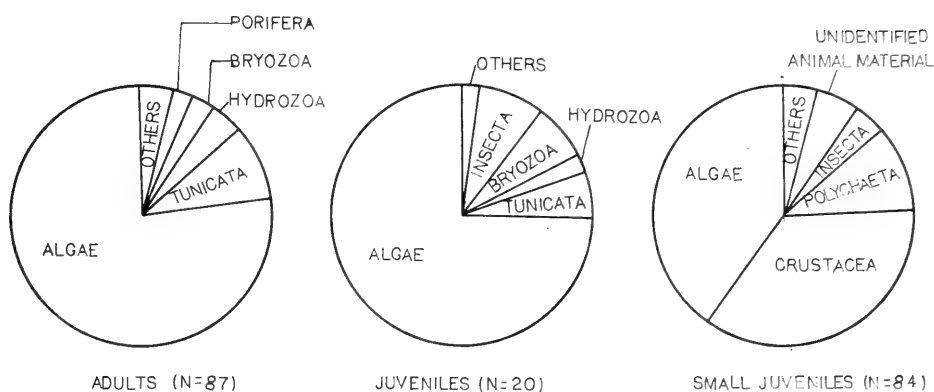
FIG. 2. Length frequency distribution in 5 mm groupings (0-4, 5-9 mm etc.) for juvenile and small juvenile *G. elevata* collected by poisoning from tidal rock pools during January 1979.

FOOD AND FEEDING OF ROCK BLACKFISH

TABLE 1. Diet of adult *G. elevata* showing seasonal variation (values expressed as percentages by estimated volume)

Food type	SPRING (n=22,1 empty)	SUMMER (n=20,1 empty)	AUTUMN (n=28)	WINTER (n=19)	FULL YEAR (n=89,2 empty)
Algae					
<i>Amphiroa</i> sp.	2.9	1.1	1.0	2.1	1.7
<i>Catenella</i> sp.	—	0.5	—	—	0.1
<i>Caulerpa filiformis</i>	—	—	—	5.5	1.2
<i>Corallina officinalis</i>	+	2.4	5.6	3.2	3.0
<i>Corallina</i> sp.	2.4	0.5	2.3	2.6	2.0
<i>Cystophora</i> sp.	1.9	—	—	—	0.5
<i>Halopteris gracilescens</i>	1.0	—	—	2.6	0.8
<i>Zonaria sinclairii</i>	12.6	—	6.5	21.8	9.9
<i>Hypnea</i> sp.	—	—	0.7	—	0.2
<i>Jania</i> sp.	1.7	—	—	—	0.4
<i>Pterocladia</i> sp.	15.5	10.1	21.9	25.3	18.4
<i>Rhodomenia</i> sp.	3.8	9.3	6.2	1.1	5.2
<i>Sargassum</i> sp.	10.2	18.3	21.8	13.7	16.4
<i>Ulva lactuca</i>	6.7	24.9	13.5	+	11.3
Unidentified algae	10.5	9.8	3.8	0.8	6.1
Total Algae	69.2	76.9	83.3	78.7	77.2
Tunicata					
<i>Didemnum</i> sp.	1.4	5.5	4.1	5.3	4.1
<i>Pyura</i> sp.	—	—	—	2.6	0.6
Salpidae	4.8	1.1	2.3	1.6	2.5
Unidentified Ascidiacea	2.3	2.9	1.8	1.8	2.2
Total Tunicata	8.5	9.5	8.2	11.3	9.4
Hydrozoa	14.4	2.9	0.1	+	4.3
Bryozoa					
<i>Celleporaria fusca</i>	0.7	—	—	—	0.1
<i>Emma crysteallina</i>	2.3	—	1.3	—	1.0
<i>Membranipora membranacea</i>	—	1.3	—	—	0.3
<i>Membranipora pillosa</i>	2.4	+	0.3	3.2	1.4
Total Bryozoa	5.4	1.3	1.6	3.2	2.8
Porifera	+	7.4	1.2	0.8	2.1
Polychaeta					
Sabellidae	—	1.0	0.5	0.2	0.5
Unidentified Polychaeta	—	—	—	+	+
Total Polychaeta	—	1.0	0.5	0.2	0.5
Crustacea					
Penaeidae	1.0	—	—	—	0.2
Amphipoda	+	+	+	—	+
Brachyura	+	—	—	—	+
Total Crustacea	1.0	+	+	—	0.2
Gastropoda	—	+	+	+	+
Bivalvia	0.5	+	0.1	+	0.1
Miscellaneous					
Sand	+	1.0	1.1	2.6	1.2
Fish scales	—	—	0.3	—	0.1
Unidentified material	1.0	—	3.6	3.2	2.1

+ = trace only

FIG. 3. Composition of the diet by major food groups for different size classes of *G. elevata*.

DIET OF ADULTS

The stomach contents of 89 adult rock blackfish were analysed and of these 87 were found to contain food. Analysis of their diet by the estimated volumetric method, along with seasonal differences in the diet, is shown in Table 1. Figure 3 shows the relative proportions of the major food groups in the diet of adult *G. elevata*.

Adult rock blackfish were found to be omnivorous, consuming principally encrusting algae (77.2%) but also encrusting fauna including tunicates (9.4%), hydroids (4.3%), bryozoans (2.8%) and sponges (2.1%). The diets of adult males and females were found to be almost identical and therefore data for the sexes were combined for all analyses.

TABLE 2. Frequency of occurrence of numbers of food types per stomach in adult, juvenile and small juvenile *G. elevata*. No. = number of fish, % = percentage of fish.

Number of food types per stomach	Adults n = 87		Adults* n = 19		Juveniles n = 20		Small juveniles n = 84	
	No.	%	No.	%	No.	%	No.	%
1	2	2.3	—	—	2	10.0	20	23.8
2	6	6.9	—	—	4	20.0	28	33.3
3	17	19.6	3	15.8	7	35.0	25	29.8
4	12	13.8	3	15.8	4	20.0	7	8.3
5	11	12.6	4	21.1	2	10.0	4	4.8
6	14	16.1	2	10.5	1	5.0	—	—
7	12	13.8	5	26.3	—	—	—	—
8	8	9.2	2	10.5	—	—	—	—
9	4	4.6	—	—	—	—	—	—
10	1	1.1	—	—	—	—	—	—
Total	87	100	19	100	20	100	84	100

* Sampled in summer (for comparison with juveniles and small juveniles).

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The frequency of occurrence of numbers of food types per stomach for adult fish is given in Table 2. Fish containing three food types were dominant and the mean number of food types per stomach was 5.1

The rectal contents of a small subsample of adult fish were examined and in each case the material therein appeared to be passing from the rectum in a fairly intact condition, with algae retaining their original shape and showing little bleaching of colour.

DIET OF JUVENILES

The stomach contents of 25 juvenile rock blackfish were analysed and of these 20 were found to contain food. The diet of juvenile *G. elevata* collected from pools at both low and high tide levels is given in Table 3. The proportions of the major food groups in the diet of juveniles is shown in Fig. 3.

TABLE 3. Diet of juvenile *G. elevata* from rock pool habitats (values for estimated volumes expressed as percentages).

Locality	Bare Island ^A	Avalon ^A	Narrabeen ^B	Combined ^{A+B}
Date	10.i.79	13.i.79	14.i.79	10.i.79-14.i.79
Number of fish	8	7,1 empty	10,4 empty	25,5 empty
SL range (mm)	73-102	90-128	80-134	73-134
Food type				
Algae				
<i>Enteromorpha intestinalis</i>	11.2	—	—	4.5
<i>Pterocladia</i> sp.	13.1	43.3	—	18.3
<i>Ulva lactuca</i>	41.3	36.7	53.4	43.5
Unidentified algae	8.7	13.3	0.8	7.8
Total Algae	74.3	93.3	54.2	74.1
Crustacea				
Amphipoda	—	0.8	—	0.2
Brachyura	—	—	18.3	5.5
Cirripedia	2.5	1.7	3.3	2.5
Total Crustacea	2.5	2.5	21.6	8.2
Bryozoa	17.5	—	—	7.0
Tunicata (<i>Pyura</i> sp.)	—	—	20.1	6.0
Hydrozoa	2.5	4.2	—	2.3
Mollusca				
Patellidae	0.6	—	—	0.2
Unidentified Mollusca	1.3	—	—	0.5
Total Mollusca	1.9	—	—	0.7
Chironomidae	1.3	—	—	0.5
Miscellaneous				
Fish scales	—	—	0.8	0.2
Unidentified material	—	—	3.3	1.0

A Pools ~ 0.6 m deep and situated near low tide level with a good cover of algae, including *Sargassum* sp., *Ecklonia radiata* and *Ulva lactuca*.

B Shallow tidal rock pools (<0.3 m deep) near high tide level, with some *Ulva lactuca* present.

Juvenile rock blackfish were also found to be omnivorous, taking mainly algae (74.1%), crustaceans (8.2%), bryozoans (7.0%), ascidians (6.0%) and hydroids (2.3%).

The frequency of occurrence of numbers of food types per stomach for juvenile fish is given in Table 2. Fish containing three food types were again dominant and the mean number of food types per stomach was 3.2.

DIET OF SMALL JUVENILES

The stomach contents of 113 small juvenile rock blackfish were analysed and of these 84 were found to contain food. The diet of small juvenile *G. elevata*

TABLE 4. Diet of small juvenile *G. elevata* from rock pool habitats (values for estimated volumes expressed as percentages).

Locality Date Number of fish SL range (mm)	Bare Island ^B 10.i.79 25,3 empty 13-28	Avalon ^B 13.i.79 19,5 empty 23-41	Narrabeen ^B 14.i.79 69,21 empty 15-55	Combined ^B 10.i.79-14.i.79 113,29 empty 13-55
Food type				
Algae				
<i>Ulva lactuca</i>	—	6.4	23.7	14.7
<i>Enteromorpha intestinalis</i>	—	52.2	3.8	10.9
Unidentified algae	30.5	3.6	9.6	13.9
Total Algae	30.5	62.2	37.1	39.5
Crustacea				
Amphipoda	0.9	12.1	10.0	8.1
Brachyura	—	—	2.7	1.5
Cirripedia	5.0	—	2.2	1.5
Copepoda	21.8	20.0	2.3	10.5
Isopoda	—	—	3.0	1.7
Unidentified Crustacea	—	5.7	20.6	12.8
Total Crustacea	27.7	37.8	40.8	36.1
Polychaeta	29.1	—	4.7	10.3
Insecta				
Chironomidae	3.2	—	4.0	4.0
Diptera	—	—	1.2	0.7
Total Insecta	3.2	—	5.2	4.7
Mollusca				
Bivalvia	—	—	1.7	0.9
Gastropoda (eggs)	—	—	1.0	0.5
Placophora	—	—	0.6	0.3
Total Mollusca	—	—	3.3	1.7
Porifera	—	—	1.0	0.6
Tunicata	—	—	0.2	0.1
Unidentified animal material	9.5	—	5.0	5.5
Miscellaneous				
Fish scales	—	—	0.2	0.1
Sand	—	—	0.4	0.2
Unidentified material	—	—	2.1	1.2

B Shallow tidal rock pools (< 0.3 m deep) near high tide level, with some *Ulva lactuca* present.

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from pools near high tide level is given in Table 4. Figure 3 gives the proportions of the major food groups in the diet of small juveniles.

Small juvenile rock blackfish were found to be omnivorous, consuming mainly algae (39.5%) and crustaceans (36.1%). Other foods included polychaetes (10.3%), insects (4.7%) and molluscs (1.7%).

The frequency of occurrence of the numbers of food types per stomach for small juveniles is given in Table 2. Fish containing two food types were dominant and the mean number of food types per stomach was 2.4.

COMPARISON OF THE DIETS OF DIFFERENT SIZE CLASSES

The major food groups in the diets of adult, juvenile and small juvenile *G. elevata* are presented in Fig. 3. Differences in the amount of plant material eaten by these size classes are shown in Fig. 4. The plot of 95% confidence intervals on Fig. 4 showed that there was no significant difference between the amounts of plant material eaten by adults and juveniles. However, there were significant differences between the amounts eaten by small juveniles and juveniles and small juveniles and adults.

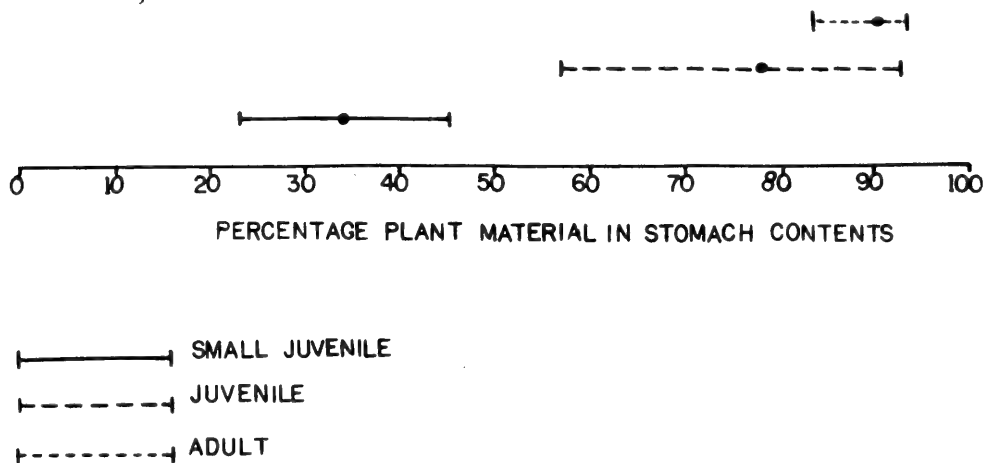


FIG. 4. Mean percentages of plant material in the stomach contents of the three size classes of *G. elevata* during summer (95% confidence limits, using arcsin transformed percentages, are shown).

The percentage of fish from each size class with a predominance of either plant or animal material in their stomachs are presented in the following tabulation:

STOMACH CONTENTS	SIZE CLASSES		
	Small juveniles	Juveniles	Adults*
Animal material	58.3	15.0	11.5
Plant material	41.7	85.0	89.5

*Summer samples only

ALIMENTARY TRACT MORPHOLOGY

The digestive tract in adult *G. elevata* is shown in Fig. 5. It is relatively long and typical of fishes with a predominantly herbivorous diet. The stomach is large and U-shaped with a muscular pyloric region. The intestine is relatively long and coiled, and there is a large but varying number of pyloric caeca (usually > 100). The small tricuspid incisors of *G. elevata* form a broad band, as in male *G. tricuspidata* (Stead, 1908), and are well adapted for tearing off and dislodging encrusting flora and fauna. The teeth appear to have a similar serial replacement pattern to that of *G. nigricans* as described by Norris and Prescott (1959). The buccopharynx and tooth pattern of *G. elevata* is shown in Fig. 6.

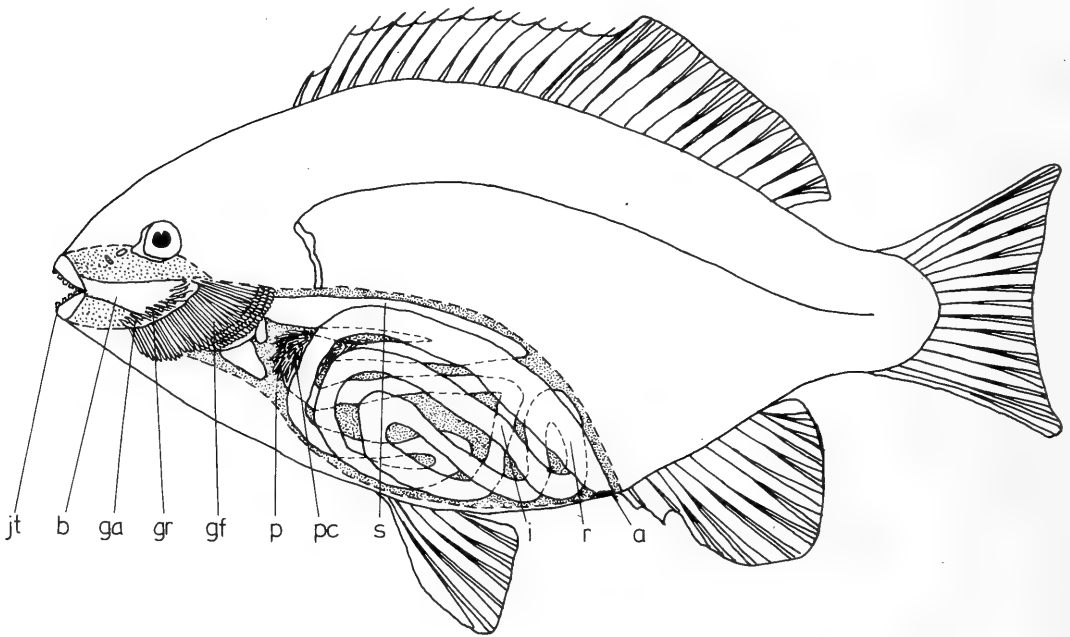


FIG. 5. Simplified diagram of the alimentary tract of *G. elevata*. a: anus, b: buccopharyngeal cavity, ga: gill arch, gf: gill filament, gr: gill raker, i: intestine, jt: jaw teeth, pc: pyloric caeca, p: peritoneal cavity, r: rectum, s: stomach.

The mean relative gut lengths for the various size classes were as follows: adults 2.1 (S.D. \pm 0.4), juveniles 1.7 (S.D. \pm 0.3) and small juveniles 1.0 (S.D. \pm 0.3). The relationship of RGL to the amount of plant material in the diet is shown in Fig. 7.

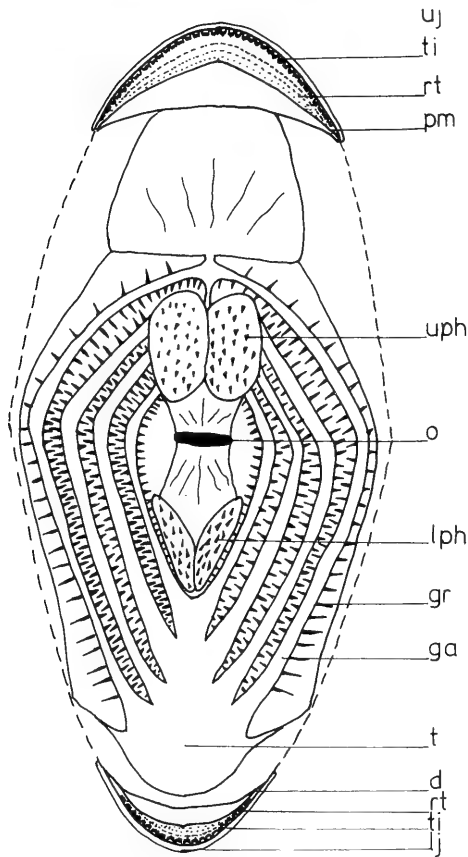


FIG. 6. Simplified diagram of the buccopharyngeal cavity of *G. elevata*. d: dentary, ga: gill arch, gr: gill rakers, lj: lower jaw, lph: lower pharyngeal tooth pad, o: oesophagus, rt: replacement teeth, ti: tricuspid incisors, pm: premaxillary, t: tongue, uj: upper jaw, uph: upper pharyngeal tooth pad.

DISCUSSION

The overall diet of adult *G. elevata* is generally similar to that found for *G. nigricans* in California (Williams and Williams, 1955) but differs from that of adult *G. tricuspidata* from rocky reefs in New Zealand (Russell, 1971), since, although the latter consumes a similar range of algae, it ingests no encrusting fauna. The results of the present study also support the brief notes of Stead (1908) who recorded *G. elevata* as feeding on "gelatinous weed" and Roughley (1951) who noted that this species ate "weed" but also took prawns, cunjevoi and other "animal fishing baits".

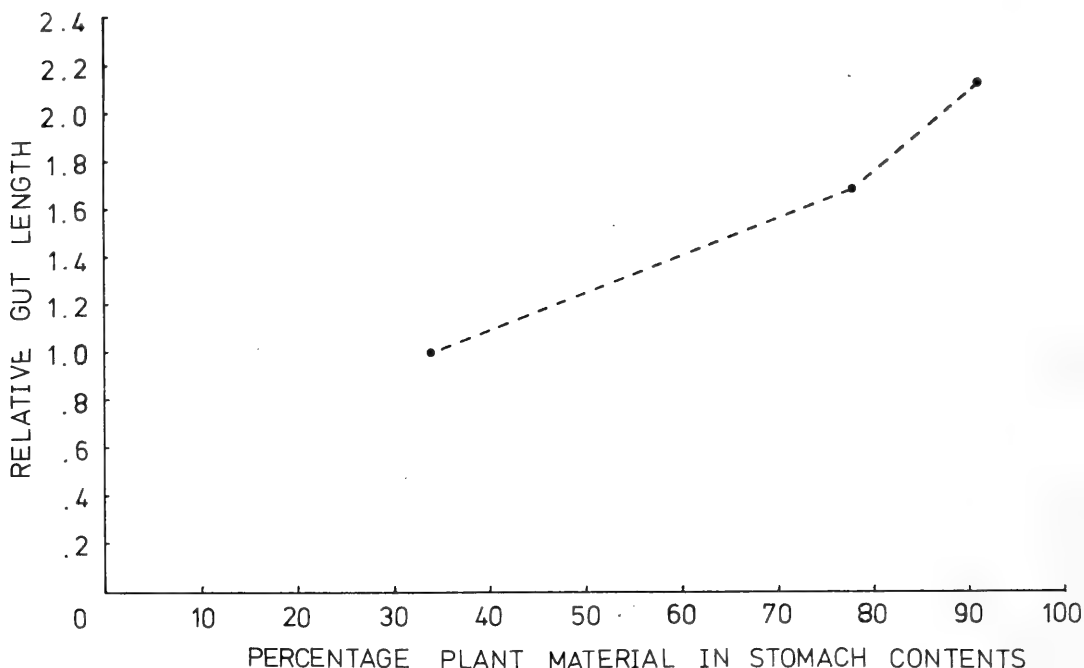


FIG. 7. The percentage volumes of plant material in the stomach contents of the three size classes of *G. elevata* in relation to changes in relative gut length. (Percentages transformed to arcsin values).

A significant difference was observed between the diet of small juveniles and that of juveniles and adults in that small juveniles consumed considerably larger amounts of animal material (Fig. 4). In addition, 58.3% of small juveniles consumed a majority of animal material while for the vast majority of juveniles and adults, plant material was predominant in the diet. The differences in diet between size classes may be related to the use of upper littoral tidal pools as "nursery areas" by small juvenile fish. These tidal pools contained both smaller numbers and fewer species of algae and higher proportions of small crustacea than the lower littoral and sub-littoral habitats occupied by the larger size classes of fish (pers. obs. authors). The adaptation of the small juveniles to a less herbivorous diet is reflected in their relatively short intestinal length when compared with the larger fish (Fig. 7).

The only noticeable difference between the diets of juvenile and adult fish was that the former ate fewer species of algae and a greater proportion of mobile fauna (Table 3) whereas the animal component of the diet in adults was made up almost entirely of encrusting fauna (Table 1). There is considerable overlap in the habitats of these two size classes during the tidal cycle (pers. obs. authors)

and this may account for their similar diets (Fig. 3). As tidal levels appear to influence which habitats the different size classes of *G. elevata* have access to, further studies need to be undertaken to determine the effect this has on their feeding behaviour.

Williams and Williams (1955) noted differences in the diets of small and large *G. nigricans*. In general they found that newly recruited juveniles (23-32 mm SL) consumed both animal and plant material while the larger fish were predominantly herbivorous. Similar results have been obtained for *G. tricuspidata* (Pollard, Bell and Burchmore, unpublished data) where small juveniles sampled from seagrass beds in Port Hacking (Sydney) were found to be microphagic carnivores, whereas the adults were herbivorous.

It appears therefore that a substantial dependence on animal foods during the early life history stages, with a change to a predominantly herbivorous diet by the larger size classes, may be typical of girellid fishes. In the case of *G. elevata* there is a noticeable increase in relative intestinal length associated with the increase in the consumption of plant material as the fish grows (Fig. 7).

According to the classification of Al Hussaini (1949), small juveniles (RGL = 1.0) should be carnivores and juveniles (RGL = 1.7) and adults (RGL = 2.1) should be omnivores. This classification does not appear to fit *G. elevata* as small juveniles are definitely omnivorous (Table 4) while adults and juveniles are also omnivores although they consume mainly algae (Tables 1 and 3). The adult intestine however shows the typically herbivorous characters of being long and coiled (Fig. 6). Burchmore (1976) described the gut of *G. tricuspidata* as being of the herbivorous type. The gut of *G. elevata* is very similar in shape to that of *G. tricuspidata* but it is slightly shorter in relative length. The teeth of *G. elevata* are highly effective for a herbivorous diet in that they are well suited to snipping and scraping encrusting organisms from the substratum.

Four species (*Pterocladia*, *Sargassum*, *Ulva* and *Zonaria*) make up the bulk of the algae eaten by adult *G. elevata* (Table 1). The various proportions of these algae in the diet changed over the study period but the combined total percentage of them consumed during any one season remained approximately constant. Thus it appears that *G. elevata* requires a certain proportion of algae in its diet and takes whatever algae are readily available in the habitat. Kilner and Akroyd (1976) also found that *G. tricuspidata* ate different plants on a seasonal basis.

Bell *et al.* (1978) found that some monacanthid fishes selected pieces of seagrass that were heavily encrusted with bryozoans and polychaetes in order to obtain the attached animal fauna as a food source. While some sublittoral algae in the Sydney region (e.g. *Ecklonia radiata*) support encrusting fauna, the species of algae consumed by *G. elevata* supported relatively little or no such fauna.

As the pieces of algae appear to pass from the digestive tract of *G. elevata* in a relatively intact condition it is unclear as to how this species derives its nutrition.

Williams and Williams (1955) noted that the bulk of the algae consumed by *G. nigricans* also passed through the alimentary tract undigested and did not appear to be greatly altered physically. Russell (1971) also found that algae consumed by adult *G. tricuspidata* showed no signs of trituration. Although the ingestion of large quantities of apparently unutilized algae thus appears to be typical of girellid fishes, it is difficult to accept that the large amounts of algae ingested by such herbivorous fishes are not an important food item *per se* (Russell, 1971). This would also appear to apply in the case of adult and juvenile *G. elevata* where ~ 75% of the diet is made up of algae.

Stickney and Shumway (1974) have shown that cellulase activity exists within the digestive tracts of several teleost species, and Conacher *et al.* (1979) demonstrated that the leatherjacket *Monacanthus chinensis* is capable of utilizing the more labile carbon compounds in both seagrass and algae. Further research on the digestive processes of girellid fishes is required to determine how, and to what extent, algae are utilized as a nutrient source.

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Some Observations on the Reproductive Biology of *Sminthopsis virginiae* (Tarragon), (Marsupialia: Dasyuridae).

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ABSTRACT

Sminthopsis virginiae is polyoestrous, like other members of the genus, and appears capable of breeding throughout the year. The reproductive condition of females can be determined readily from examination of the pouch. Male-female interactions are agonistic except during oestrus when females become sexually receptive and attract males by calling. This elicits similar calling and searching behaviour in males.

The gestation period is in the range 13-20 days. Young are carried in the pouch for 55 days then left in a nest built under debris. They become independent of the mother at about 90 days old. Six types of call have been recorded: four of them involved in female-juvenile interactions.

INTRODUCTION

Sminthopsis virginiae (Tarragon), Family Dasyuridae, is a terrestrial, carnivorous marsupial of Australia and New Guinea, which grows to the size of a small rat (Plate 1). Though first described in 1847, it has remained little known and poorly represented in museum collections.

The only published notes on its biology are brief comments on its burrowing habits (Collett, 1887; Lumholtz, 1889) and its apparent preference for sunny areas in open forests (Tate, 1952). Nothing has been recorded on its reproductive biology and knowledge of reproduction in other members of the genus is restricted to field and laboratory studies of *S. crassicaudata* (Martin, 1965; Ewer, 1968; Godfrey, 1969a; Smith and Godfrey, 1970; Godfrey and Crowcroft, 1971; Morton, 1978b) and a laboratory study of *S. macroura* (= *S. larapinta*) by Godfrey (1969b). The capture of three adult *S. virginiae* in 1976 and 1977 and their successful breeding in captivity allowed a preliminary investigation of their reproductive biology.

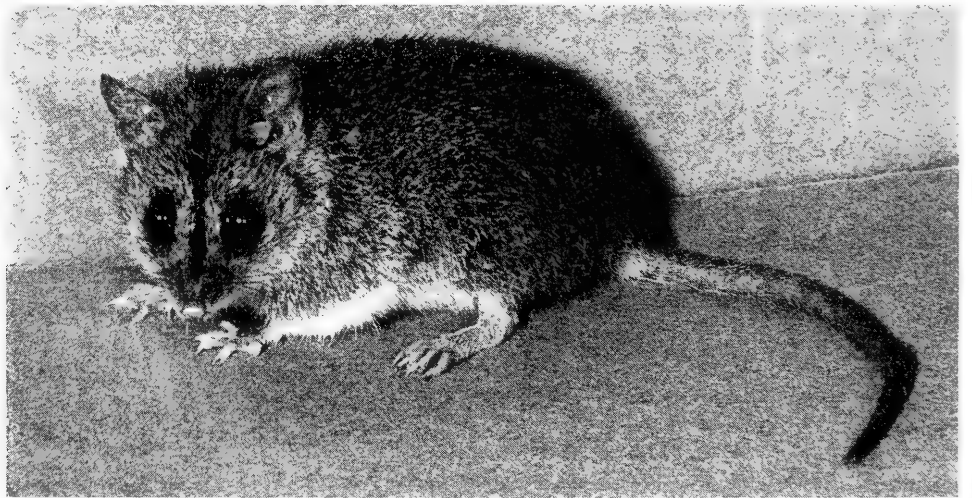


PLATE 1. Adult female *Sminthopsis virginiae* (Upper photo courtesy of Queensland Museum).

REPRODUCTION IN *SMINTHOPSIS VIRGINIAE*

MATERIALS AND METHODS

Two mature *S. virginiae* (A1 and A2, Table 1) were hand-caught on separate occasions near Kennedy, North Queensland (Lat. 18° 10'S; Long. 145° 56'E) in August, 1976. Both were found sheltering under logs on a railway easement which had a ground cover of eucalypt saplings and blady grass. The surrounding vegetation was a low, open forest of *Melaleuca viridiflora* and *Eucalyptus polycarpa* with dense understoreys of shrubs, grasses and leaf litter. A third mature *sminthopsis* was trapped in dense blady grass on a river flat on the Lockhart R., Cape York Peninsula (Lat. 13° 05'S; Long. 142° 30'E) in August, 1977 by the Queensland National Parks and Wildlife Service. All three are referable to nominate *S. v. virginiae* of Archer (in prep.). Five litters were subsequently born in captivity and three of these litters were reared to maturity (Table 1).

TABLE 1. Details of *Sminthopsis virginiae* individuals studied.

Animal	Sex	Approximate Date of Birth	Parents	Notes
A1	F	—	—	Collected Kennedy
A2	M	—	—	Collected Kennedy
A3	F	23.x.76	A1, A2	
A4	F	23.x.76	A1, A2	
A5	F	23.x.76	A1, A2	
A6	M	14.iv.77	A1, A2	
A7	F	14.iv.77	A1, A2	
A8	M	—	—	Collected Lockhart R.
A9	M	29.xi.77	A3, A8	
A10	F	29.xi.77	A3, A8	
A11-A15	?	27.xii.77	A4, A8	Eaten (?) 13.i.78
A16	?	30.i.78	A4, A8	Eaten (?) 12.ii.78
A17	?	30.i.78	A4, A8	Died 27.iii.78

Adult *S. virginiae* were normally housed individually in glass aquaria from 60 x 30 x 30 cm to 140 x 45 x 45 cm in size. Siblings were occasionally kept together after weaning. Cages were floored with soil and leaf litter and provided with logs, bark sheets or dry grass for shelter. The animals were fed a finely minced mixture of heart, liver, brain, steak, dog biscuit and egg, similar to that described by Collins (1973). This was supplemented occasionally with insects, frogs, lizards, snakes and mice. Fresh water was supplied daily.

Behavioural observations were made under dim artificial lighting over periods of one to four hours at various times between 1900 hr and 0400 hr. In addition, the animals were kept in the author's study for over two years, enabling daily, casual observations of activity. Particular emphasis was placed on recording sexual activity. It is estimated that several hundred hours were spent observing their

behaviour. Tape recordings of vocalisations were made during observation periods using a Hitachi D500 cassette recorder and a Tandberg 11 tape recorder with a Sony ECM33 microphone.

Development of the pouch young was monitored during the rearing of three litters born 29-11-77, 27-12-77 and 30-1-78 (Table 1). The first two litters were allowed to develop with minimal disturbance. The observations of developmental stages summarised in Table 2 were made with the unaided eye on animals attached to nipples but everted from the pouch. Measurements of pouch young and adults were made with vernier calipers and dividers. Crown-rump length (CRL) was measured between 1 and 25 days of age; after this the wriggling of the young introduced serious errors. Head length (HL) was measured from 18 days old onward, except between 50 and 60 days old. During this period, either the young could not be removed from the pouch without injury, or they had just been left in the nest and were particularly sensitive to disturbance.

RESULTS

SOCIAL AND MATING BEHAVIOUR

Adult male and female *smynthopsis* were housed separately, as they squabbled continuously when kept together. This was especially true of the wild-caught animals. The only notable exception to this occurred in June, 1978 when A4 and A5 (sibling females) were accidentally allowed into the same cage and exhibited little of the expected aggressive behaviour. A6 (non-sibling male) was introduced to their cage the following day and the three animals were housed together for four months without the usual incessant threat calls and fighting. However, while it was common to find the females sleeping together, the male was never observed sleeping with either of them and was regularly chased and bitten if he ventured close to them. There was no evidence of sexual activity at any stage.

During aggressive male-female interactions, both animals utter a series of drawn-out, rasping 'tzzzz' calls, increasing in intensity as the distance between them decreases. At the same time, the ears are flattened, the teeth bared and the body pressed close to the ground. It is usual for the male to approach the female and be chased and bitten by her if he comes too close. However, during brief periods of sexual receptivity, the female becomes very active and scurries about, sniffing the air while standing erect and emitting loud 'tsst' calls (referred to here as oestrous calls) at irregular intervals of 2 to 10 seconds. Nearby males respond with similar calls and likewise scurry about, sniffing the air, and apparently searching for the calling female. The male's call could not be distinguished by ear from the female's and the *smynthopsis* do not appear to distinguish between them either, since both sexes will respond to tape recordings of male or female oestrous calls and even to a human imitation of them. Male *smynthopsis* were never observed to initiate a bout of calling.

The reciprocating call routine usually starts at dusk and lasts from one minute to several hours. Calling ceases immediately a member of the opposite sex is introduced to the cage. Once together, mating is virtually immediate, and no oestrous calling is heard while the animals are together.

Once the male contacts a receptive female, there are few preliminaries to mating. The male commonly rushes over to the female, seizes her by the scruff of the neck, and attempts copulation immediately. If he is wary of approaching her, the female may sidle up to him with ears depressed, fur flattened, body pressed close to the ground, and without uttering the usual threat call. The male responds by baring his teeth and uttering a mild threat call until the female is close, when a brief olfactory inspection is followed by copulation.

Copulation is violent and prolonged. Early in the study, matings were interrupted after two to three hours because it was feared the female might be killed if unable to escape. However, in six later matings, the animals remained together overnight. Matings were not timed regularly, but one lasted over seven hours. During mating, the male *smintopsis* grasps his partner firmly around the lower abdomen with his forepaws and rubs his chin vigorously along her back and nape. This rubbing appears to induce passiveness in the female. Copulation is interrupted at irregular intervals of 15 seconds to 10 minutes either by threat calls and struggling from the female or by brief bouts of genital licking by both animals. When the female struggles, the male wrestles her into submission, intensifies his neck-rubbing, and often grips the female's neck with his teeth, causing extensive hair loss and scarring.

If left together overnight, the *smintopsis* usually squabble the next day, particularly if the male shows further sexual interest in the female. It was suspected that one night of uninterrupted mating might inhibit further oestrous calling by the female. However, females showed further calling in four cases out of six in which a pair were left together overnight and separated the following day.

OESTROUS CYCLE

Detailed records of oestrous calling were kept over a two year period. Bouts of calling lasting from one to seven days were associated with a marked swelling, flushing and lubrication of the vagina and with sexual receptivity. The time between the first day of one bout of calling and the first day of the next bout has been used as an estimate of the length of the oestrous cycle.

A5 came into oestrus six times between December, 1977 and June, 1978 at intervals of 31, 29, 32, 40 and 39 days. She was mated on every occasion but apparently failed to produce young. A4 showed two consecutive cycles of 34 and 29 days duration before producing two young in December, 1977. A3 showed a single cycle of 34 or 38 days before producing young in November, 1977: the doubt arises from difficulty in determining which animals were calling one evening.

Oestrous calling was noted in every month except August and September and litters were born in January, April, October, November and December.

Periods of anoestrus from two to six months duration were common. Lactating females remained anoestrous until the young were close to weaning or died. For instance, A1 produced two litters which were both weaned at about 80 days of age and she was noted calling at 75 and 89 days respectively. During the second half of 1978 most females showed little or no oestrous calling and those that did were hostile toward the males when mated. No litters were born after January, 1978. A dietary problem may have caused this as the *Sminthopsis* were receiving no live food at this time and all died eventually during 1978.

POUCH CHANGES DURING OESTRUS AND PREGNANCY

The pouch of juvenile and anoestrous *S. virginiae* is crescentic with an anterior opening (Figure 1a), but its shape changes markedly during the oestrous cycle and gives an indication of the reproductive status of females.

Between 10 and 20 days after the onset of oestrus (as indicated by oestrous calling) the pouch walls become swollen and flushed red while the anterior wall becomes prominent (Figure 1b). This is followed closely by the development of

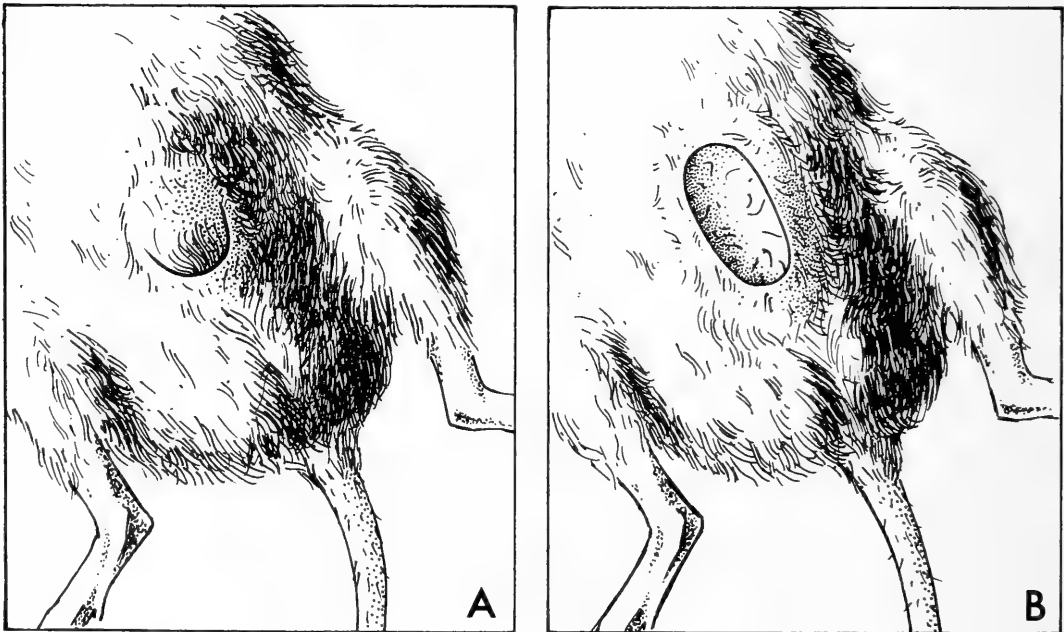


FIG. 1. Pouch configuration in *Sminthopsis virginiae*
A: juveniles and anoestrous females
B: oestrous females and those carrying young

skin folds and papillae in the mammary region, accompanied by a thinning out of the dense patch of hair which entirely obscures this area in regressed pouches. The eight nipples, though remaining very small, become pink and finally bright red for a day or two about 18-22 days after the onset of oestrus.

In females that do not bear young, the pouch develops these features between 10 and 20 days and regresses to its original condition between 20 and 30 days after the onset of oestrus. However, the pouch does not regress until after weaning in females that produce young. Rather, its walls develop markedly — particularly the anterior lip — and the nipples on which young are suckling become pale, swollen and elongate, remaining like this until the young are weaned. Nipples not being suckled remain small and pale.

The pouch regresses after weaning to the condition shown in Figure 1a, except that the anterior lip remains as a low ridge and the pouch walls are slightly swollen, though pale. This condition persists after several months of anoestrus and distinguishes females which have borne young from those which have not. In the latter the pouch walls are thin and pale and there is no anterior ridge. Post-weaning regression of the pouch takes 15-20 days.

GESTATION PERIOD

The gestation period could not be well defined in this study. After three matings the pouch was examined daily between days 10 and 22 and every 2-3 days thereafter. No young were found, so inspections were limited to once every 2-3 days after later matings to reduce disturbance of the adults. From 17 matings only 5 litters were observed. Gestation periods for three of these were 13-16, 16-19 and 17-20 days.

GROWTH AND DEVELOPMENT OF THE YOUNG

Only three litters were available for study of the pouch young and only one of these litters was reared to maturity. Crown-rump length of three *sminthopsis* is plotted against age in Figure 2a for the first 25 days of development. Head-length versus age is plotted for the same three animals from 18 days to adulthood in Figure 2b. Unfortunately, the only animal for which a reasonably complete set of measurements was collected, (A9), developed with a deformed snout. This is reflected in its relatively short adult head length but the deformity appears not to have affected markedly the earlier stages of development.

The major developmental stages of the pouch young are summarised in Table 2. Many features could have been distinguished somewhat earlier had it been possible to remove young at regular intervals for closer examination. However, Table 2, in conjunction with Figure 2, does provide a means of estimating the age of pouch young.

The young were first left on their own in the nest at 55-56 days of age and began exploring outside it about 10 days later. They were first seen eating solid

REPRODUCTION IN *SMINTHOPSIS VIRGINIAE*

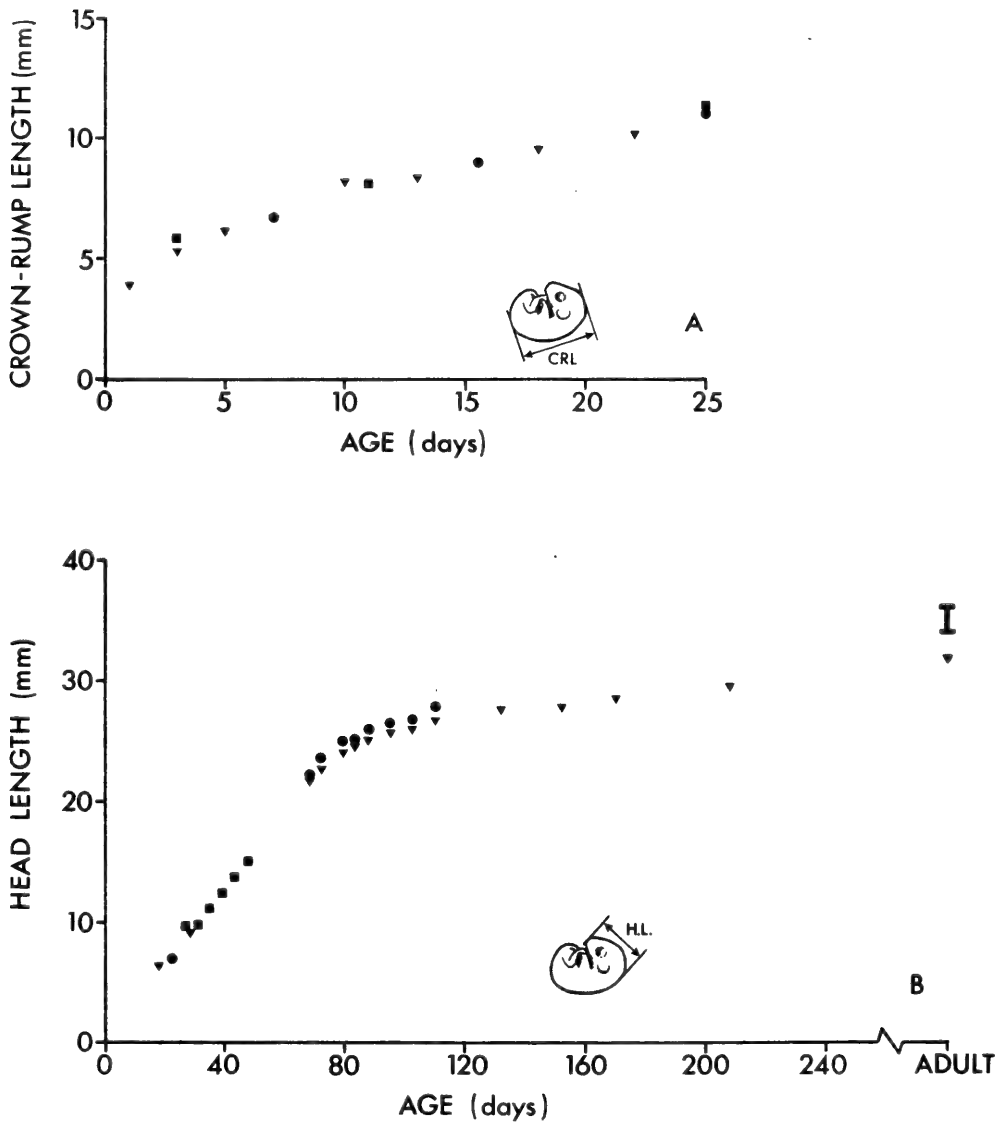


FIG. 2. Growth curves of *Sminthopsis virginiae*

A: Crown-rump length (CRL) against age of pouch young

B: Head length (HL) against age of juveniles

▼ - A9; ● - A10; ■ - A11

I - Range of head lengths in adults

REPRODUCTION IN *SMINTHOPSIS VIRGINIAE*

TABLE 2. Developmental stages of pouch young of *S. virginiae*.

AGE (days)	Forelimbs	Hindlimbs	Eyes	Mouth	Ears	Fur
0	Prominent. No finger buds.	Not visible.	Not visible.	Circular.	Not visible.	Naked. Pink.
5			Minute black spots.			
10		Approx. 2/3 of forelimb length.				
13	Finger buds appear.	Feet and toe buds appear.				
16			Transparent corneal disk appears.			
18	Digits separated.					
20	Elbow and wrist movements seen.		Eyelids begin to form. No slit.		Pale bulge on head.	
22		Toes separate. Knee and ankle movements seen.				Some grey pigmentation on head.
25	Fingers able to grip pouch hair.					
28	Claws visible on fingers.		Eyelid slit forms. Cornea visible below eyelids.	Mouth slit reaches to below front of eye.	Pinna developing.	Hair appearing on head. Hair papillae all over body.
34					External pinna measurable—2mm deep.	
38		Claws visible on toes.				Vibrissae 2-3mm long. Head and dorsum with thin, dark hair. Sparse hair on rump and venter.
40-45				Mouth slit opening to front of eye.		
50-55				Mouth slit opening to back of eye.	External pinna 5-6mm deep.	Completely furred. Light hair on feet, forelimbs and venter. Tufts on ears.
56-58			Eyes open.			

food at 74-78 days old and were weaned between 80 and 90 days of age. By this time, they had a snout-vent length of 85-90 mm, a total length of 185-190 mm and a weight of 18-20g. They grew slowly after weaning and attained their adult size of 120-130 mm snout-vent length, 230-240 mm total length and 40-50g weight at about 200 days.

SEXUAL MATURITY AND LONGEVITY

The earliest age at which oestrous calling occurred in females was 230 days (A7). A3, A4 and A5 were first noted calling at 347, 347 and 413 days old respectively. The scrotum of A9 reached adult size at about 200 days old. Thus a very rough estimate of about 200 days can be suggested for sexual maturity of both sexes in *S. virginiae*.

Laboratory-bred animals reached adult size at about 200 days old. A1, A2, and A8 (all mature when caught) lived 480, 360 and 300 days respectively in captivity. Thus a lifespan of at least two years is indicated.

NESTING AND BURROWING

Nest-building activity was seen only in female sminthopsis after carrying young for 50-55 days when they were getting too big to be carried in the pouch. At such times the females gathered leaves, grass and bark which were arranged in a rough saucer-shaped depression under a log or piece of bark. Males and females without young showed little or no nest-building activity: at most they would gather a few pieces of grass or leaves to form a thin ground cover under a log.

Attempts to stimulate burrowing activity by providing the sminthopsis with deep, compacted soils were unsuccessful in both males and females at all stages of the oestrous cycle. This was the case regardless of whether or not shelter was provided. In contrast, native rodents (*Pseudomys delicatulus*), tested under similar conditions, burrowed extensively.

VOCALISATIONS

Adult sminthopsis without young produce relatively few calls apart from a variety of very faint squeaks and snuffles while eating and exploring. However, vocal communication plays an important role in mating and rearing of the young.

The oestrous and threat calls have been described above. The female sminthopsis also utters calls similar to the oestrous call, but lower in intensity, in three different contexts. When entering the nest or when passing it while the young are hidden there, the female utters one or two faint "tsst" calls. It is not known if the young respond to these calls. If the mother is suckling the young in the nest and one strays away, she utters a louder "tsst" to which the young responds by scampering rapidly back into the nest. A call of the same intensity is uttered when the mother carries the young on her flanks and one falls off. The

juvenile emits a very loud, rapid chatter — "tz-tz-tz-tz-tz" — to which the female responds by stopping, turning to the juvenile and uttering the "tsst" call while lowering her rump. The juvenile runs to the mother, who assists it in climbing onto her flanks by pushing it up with her nose. As the young approach the age of weaning, the mother increasingly ignores their distress calls, forcing them to run after her. The rapid chatter of juveniles disappears a few weeks after weaning.

DISCUSSION

The oestrous call and its associated behaviour described here have not been reported for any other species of *Sminthopsis*. However, S. van Dyck (pers. comm.) has observed very similar behaviour in *S. murina*. He describes their calls as a "wheezy, husky 'chee'" on the first few days of calling, changing to "a succession of sharp 'ts-ts-ts-tsst'" calls after about five days in unmated females. It is possible that this behaviour is more widespread among members of the genus but has not been noted where animals were kept as pairs or small groups. Morton (1978a) found that *S. crassicaudata* had a very loose social organisation in the wild and the observations reported here suggest that *S. virginiae* also conforms to this pattern. Thus, oestrous calling and its associated searching behaviour may be a mechanism for bringing these apparently solitary animals together for mating in the dense undergrowth where they live.

S. virginiae is polyoestrous, as are the other two members of the genus studied to date (Woolley, 1973), and this study showed also year-round sexual activity. This is rather surprising given the markedly seasonal nature of their sub-tropical habitat and the prevalence of wet-season breeding in many animals of this region (pers. obs.). Interestingly, Aslin (1975) found both wild and captive *Planigale maculata* (= *Antechinus maculatus*) breeding during the dry season in sub-tropical northern Australia. It is possible that more observation may show both species to be predominantly summer breeders.

The form of the pouch in juvenile and non-oestrous adult *S. virginiae* fails to conform to any of the four pouch types described from dasyurids by Woolley (1974). However, at some stages of the oestrous cycle and during pregnancy, it conforms to Woolley's Type 3 pouch, typical of both non-pregnant and pregnant *S. crassicaudata* and *S. macroura*. The marked changes in pouch conformation in *S. virginiae* appear to make it a much better indicator of the reproductive state of females than is the case for *S. macroura* (Godfrey, 1969b).

The observation that male *S. virginiae* use a neck grip during copulation is of interest since Ewer's (1968) observations indicated that this is not the case in *S. crassicaudata*. Ewer drew upon this fact and the differences in young-carrying behaviour between *Sminthopsis crassicaudata* and many placental mammals (which use a neck grip during copulation and when carrying young) to suggest that the

two neck-grip behaviours are closely correlated. Such a supposed correlation breaks down in the case of *S. virginiae*.

Burrowing behaviour has been reported twice for *S. virginiae*. Both Collett (1887) and Lumholtz (1889) reported that the single animals they collected were dug out of the ground. All efforts to elicit burrowing in captivity during this study were singularly unsuccessful. They did not even turn over the soil or dig in the corners of their cages. Doubt therefore remains as to whether *S. virginiae* does in fact burrow in the wild, though it may shelter in the burrows of other animals.

ACKNOWLEDGEMENTS

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Recent Records of the Australian Grayling *Prototroctes maraena* Günther (Pisces: Prototroctidae) with Notes on its Distribution

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ABSTRACT

Details of 62 collections of *P. maraena* consisting of 2080 specimens sampled from 32 different localities throughout New South Wales, Victoria and Tasmania between 13 December 1975 and 27 March 1980 are presented. The distribution of these records, which include 20 new localities, is compared with the "historical" distribution of *P. maraena*. Possible reasons for differences between past and present distributions of Australian grayling include habitat alteration, dam construction and increased research on coastal streams thus locating *P. maraena* in previously uncollected areas.

INTRODUCTION

The Australian grayling *Prototroctes maraena* Günther is known only from south-eastern Australia including Tasmania. Lake (1971) considered *P. maraena* to be the Australian freshwater fish most seriously threatened with extinction, however, it is now generally regarded as being rare (McDowall 1976). It is the only extant member of the family Prototroctidae as *P. oxyrhynchus* Günther, previously known only from New Zealand, has not been reliably recorded since 1923 and therefore is presumed extinct. Allen (1961) presented some possible reasons for the disappearance of *P. oxyrhynchus*.

Little is known of the biology of Prototroctidae. McDowall (1976) synthesised the existing knowledge on these fishes and discussed the reasons for their decline. Jackson (1976) and Bishop and Bell (1978b) have described aspects of the biology of *P. maraena*. However, basic biological data such as the exact

extent of its distribution, its migratory behaviour, the nature and location of spawning sites and juvenile habitat requirements remain unknown.

McDowall (1976) produced the only known distribution map of *P. maraena*. This map was based on collections (from 36 localities) carried out by numerous workers between 1869 and 1975. Several historical records were included and, in nearly all cases, the numbers of specimens collected were small.

Since McDowall's (1976) study the authors and other workers have collected additional records of this species, including several from new localities and some large collections such as the 312 specimens collected by Bishop and Bell (1978a). These recent records are presented and compared with the information supplied by McDowall (1976) (to which have been added a few additional historical records) in an attempt to examine any distributional changes.

Because of the apparent scarcity and instability of grayling populations it was felt that a detailed documentation of the present distribution of records of this species was essential.

MATERIALS AND METHODS

Various methods were employed by the authors to collect *P. maraena* from coastal rivers in south-eastern New South Wales, Victoria, and Tasmania. These included electrofishing (Vic. and Tas.); poisoning with rotenone, at a concentration of ~ 0.5 ppm neutralised with potassium permanganate below the sampling site (Vic.); gill nets (N.S.W. and Vic.); seine nets with a stretched mesh size of 1.5 cm (N.S.W., Vic. and Tas.) and fyke nets (Vic.). Sampling methods for each collection are listed in Tables 1, 2 or 3. A few collections by other workers were also collated by the authors and are incorporated in this paper.

Each fish was measured to the nearest mm caudal fork length (LCF) with the exception of specimens collected by P.R. Last which were measured to the nearest mm standard length (SL). In several instances water temperature, salinity (when sampling sites were not freshwater), sexual maturity and other basic biological observations were recorded with each collection. Specimens were released alive where possible. When damaged during collection or when they represented new records, they were kept and preserved in 4% formaldehyde. The collections made by T. M. Berra (Table 2) were also kept for later analysis as part of a one year study designed to elucidate the spawning localities and movements of *P. maraena* in the Tambo River and in other streams entering Gippsland Lakes, Victoria.

Preserved specimens collected in N.S.W. were lodged with the Australian Museum, Sydney; those collected in Victoria were placed in the National Museum of Victoria, Melbourne and those in Tasmania have been lodged with the Tasmanian Inland Fisheries Commission, Hobart.

RECENT GRAYLING RECORDS

RESULTS

NEW SOUTH WALES

A total of 571 grayling (excluding an unconfirmed report of approximately 10 specimens from the Tantawangalo River) were collected from 5 localities on 8 occasions between 29-11-76 and 27-3-80. Table 1 details these collections. The distribution of *P. maraena* in New South Wales, determined from these records and the data from McDowall (1976) is shown in Figure 1. A single specimen of *P. maraena* collected by Stead (undated) from the Grose River (Fig. 1:1) measuring 185 cm LCF, which is presently lodged with the California Academy of Sciences, is the only additional historical record. An unconfirmed report from a senior fisheries inspector indicates that grayling were common in the Grose River during the 1950's. Thus the Grose River appears to represent the most northerly record in Australia.

The records from the Clyde River (8) and its lower tributary the Buckenbowra River (9) are the first for these rivers. The first collection from the Brogo River (12) is also a new record although McDowall (1976) reported *P. maraena* from the Tantawangalo River (13) which is part of the same drainage system (see Fig. 1).

VICTORIA

A total of 1449 grayling were collected from 17 localities on 38 occasions between 23-2-76 and 30-11-79. These data include all collections made by T. M. Berra from the Tambo River between 15-2-79 and 30-11-79. The Tambo River collections were made from approximately 3 km of river above 'Bruthen' to the junction of the Haunted Stream. For convenience this section of river has been regarded as one "locality" (Fig. 2:8). Details of the Victorian collections are presented in Table 2, and for convenience collections from the Tambo River "locality" have been grouped into monthly "collections". The distribution of *P. maraena*, compiled from these records and the data from McDowall (1976) is shown in Fig. 2. A record of 9 specimens with an LCF range of 167-228 mm caught in the Bunyip River (Fig. 2:21) on 8 and 9-3-1903, lodged with the National Museum of Victoria is the only additional historical record.

The collections from the Nicholson (9), Avon (13), McAlister (16), Tarra (18), Albert (19), Agnes (20), W. Tarwin (21), Lang Lang (23) and Hopkins (30) Rivers, and Merriman's (17) and Warkins (22) Creeks, all represent new records (see Fig. 2).

TASMANIA

A total of 60 grayling were collected from 10 localities on 17 occasions between 13-12-75 and 29-3-79. Table 3 details these collections. The distribution of *P. maraena* determined from these records and the data from McDowall (1976) is shown in Fig. 3. A Tasmanian Inland Fisheries Commission record of one

TABLE 1. Recent records of *P. maraena* from New South Wales (i.e. post McDowall 1976).

Date	Locality	No. of Specimens	LCF range (mm)	Collection method	Collector	General Comments
29.xi.76	Shoalhaven R. below Tallowa Dam	312	113-219	See Bishop and Bell (1978a) re fish mortality	Bishop and Bell	See Bishop and Bell (1978a)
22.xii.76	Shoalhaven R. below Tallowa Dam	2	79-141	See Bishop and Bell (1978a) re fish mortality	Bishop and Bell	See Bishop and Bell (1978a)
15.xii.78	Shoalhaven R. below Tallowa Dam	8	70-81	Seine	Bell	
16.xii.78	*Clyde R. at 'Yadboro'	1	75	Seine	Bell	
16.xii.78	*Buckenbowra R. at 'Buckenbowra'	2	~210-220	Gill net	Harris	**24.0°C
28.xii.78	Tantawangalo Ck (tributary of Bega R.)	10	~220	Hook and line	Unconfirmed report from Fisheries Inspector	
1.i.79	Clyde R. 4 km downstream from 'Yadboro'	1	210	Hook and line	Ritchie	
29.i.79	*Brogo R. at Pacific Highway	3	88-94	Seine	Bell	24.5°C
27.iii.80	Brogo R. below Brogo Dam	232	150-249	Rotenone	Richardson	

* New records for N.S.W.

** Water temperatures

RECENT GRAYLING RECORDS

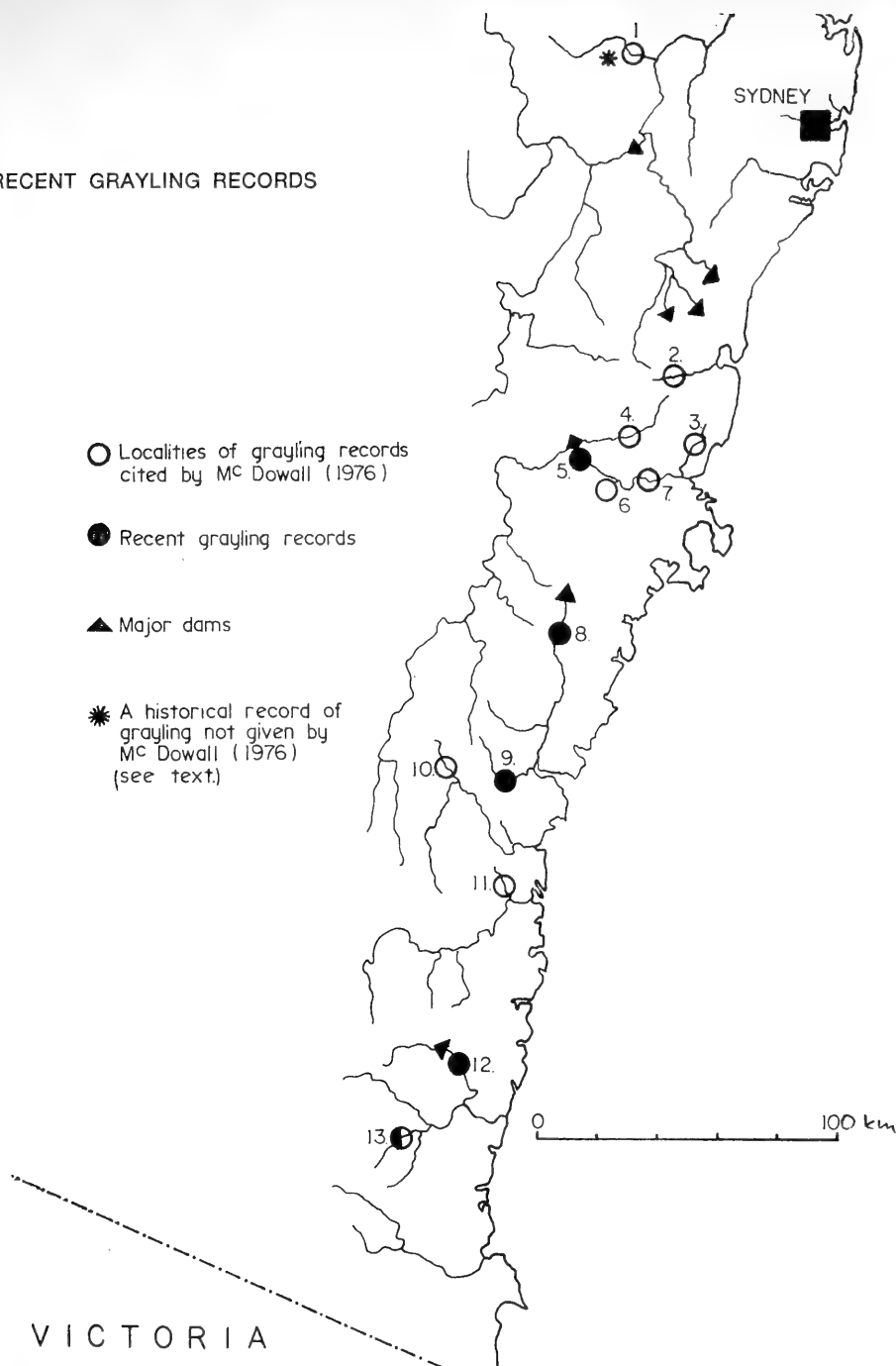


FIG. 1. Distribution of *P. maraena* in N.S.W., mapped from recent records and those cited by McDowall (1976). 1. Grose River; 2. Macquarie Rivulet; 3. Broughton Creek; 4. Kangaroo River; 5. Shoalhaven River below Tallowa Dam; 6. Yalwal Creek below Danjera Dam; 7. Shoalhaven River near 'Nowra'; 8. Clyde River near 'Yadboro'; 9. Buckenbowra River at 'Buckenbowra'; 10. Deua River at 'Araluen'; 11. Gulph Creek, tributary of Tuross River; 12. Brogo River; 13. Tantawangalo Creek, tributary of Bega River.

TABLE 2. Recent records of *P. maraena* from Victoria (i.e. post McDowall 1976). Distances given are approximations. (R = Rotenone; G = Gill net; E = Electrofishing; F = Fyke net; S = Seine net; HL = Hook and line)

Date	Locality	No. of Specimens	LCF range (mm)	Collection method	Collector	General Comments
23.iii.76	*Merriman's Ck., near 'Seaspray'	3	~190	R	VFWS [†]	**23.5°C
13.iii.77	Tambo R.	10	194-203	G	VFWS	
27.v.77	Wonnangatta R. near 'Dargo'	3	185-200	R	VFWS	
9.ii.78	Tambo R.	3	189-203	G	VFWS	21.0°C
16.i.79	Buchan R. at 'Sunny Point'	95	72-215	R	VFWS	26.5°C
17.i.79	Tambo R.	41	74-223	R	VFWS	26.0°C
23.i.79	*Albert R. above rd. bridge to 'Alberton West'	1	134	R	VFWS	27.0°C
25.i.79	*Agnes R. above Stn, Gippsland Hwy.	1	69	R	VFWS	23.0°C
12.ii.79	*Lang Lang R. at Heather Hill Crossing	29	76-86	R	VFWS	23.0°C
15.ii.79	Buchan R. at 'Sunny Point'	2	81-83	E	Berra	22.0°C
15-28.ii.79	Tambo R.	5	170-209	G	Berra	21.5°C
18.24.iii.79	Bunyip R. at 'Iona'	9	84-168	E	Hortle	19.0°C. Ripe ♀ and ♂
22.iii.79	Haunted Str. 11 km above Omeo Hwy.	2	115-119	E	Berra	16.0°C
22.iii.79	*Nicholson R. 1 km above Sarsfield Bridge	1	93	G	Berra	19.0°C
1-29.iii.79	Tambo R.	19	88-197	G,F,E	Berra	16.0-22.0°C. Ripe ♀ and ♂
4.iv.79	*Hopkins R. below Hopkins Falls	9	150-195	R	VFWS	17.0°C. Ripe ♀ and ♂
5.iv.79	*Watkins Ck. tributary of W. Tarwin R.	4	91-104	E	VFWS	
5.iv.79	Buchan R. at 'Sunny Point'	1	115	F	Berra	18.0°C
27.iv.79	*West Tarwin R. above Berry's Ck. Junction	1	~100	E	VFWS	
10-24.iv.79	Tambo R.	47	97-215	G,F	Berra	13.5-18.0°C. Ripe ♀ and ♂
9.v.79	W. Tarwin R.	1	100	F	VFWS	11.0°C
1-31.v.79	Tambo R.	115	100-222	G,F	Berra	8.0-13.0°C. Ripe fish present till 8.v.79, then spent
8.vi.79	Rainbow Ck. at junction of Thompson R.	1	130	E	Berra	10.1°C
22.vi.79	Mitchell R. at 'Tabberabbera'	3	127-133	G	Berra	10.0°C
1-30.vi.79	Tambo R.	45	116-225	G,F	Berra	6.3-10.5°C. Spent ♀ and ♂
8.vii.79	Bunyip R. at 'Iona'	1	110	E	Hortle	10.0°C
3.vii.79	Haunted Str. 15 km above Omeo Hwy.	8	122-140	F	Berra	5.0°C
22.viii.79	*Tarra R., 12 km above 'Yarram'	1	113-234	G,F,S	Berra	5.2-6.8°C
1-31.vii.79	Tambo R.	23	130	F	Berra	7.0°C
21.viii.79	Haunted Str. 15 km above Omeo Hwy.	1	114	E	Sanger	
1-31.viii.79	Tambo R.	65	119-253	G,F,S	Berra	6.5-10.5°C
6.21.ix.79	Bunyip R. at 'Iona'	5	100-112	E	Hortle	10.0°C
20.ix.79	Mitchell R. at 'Tabberabbera'	4	128-133	F	VFWS	
1-30.ix.79	Tambo R.	44	121-230	G,F,S	Berra	10.0-14.0°C
6.x.79	*Avon R. at 'Stratford'	1	210	HL	Felst	
1-31.x.79	Tambo R.	141	133-227	G,F,S,R	Berra	13.0-18.5°C
15.xi.79	*McAlister R. at 'Maffra'	1	136	F	?	
1-30.xi.79	Tambo R.	703	83-238	G,S,R	Berra	18.7-20.0°C

* New records for Victoria

† Victorian Fisheries and Wildlife

** Water temperatures

RECENT GRAYLING RECORDS

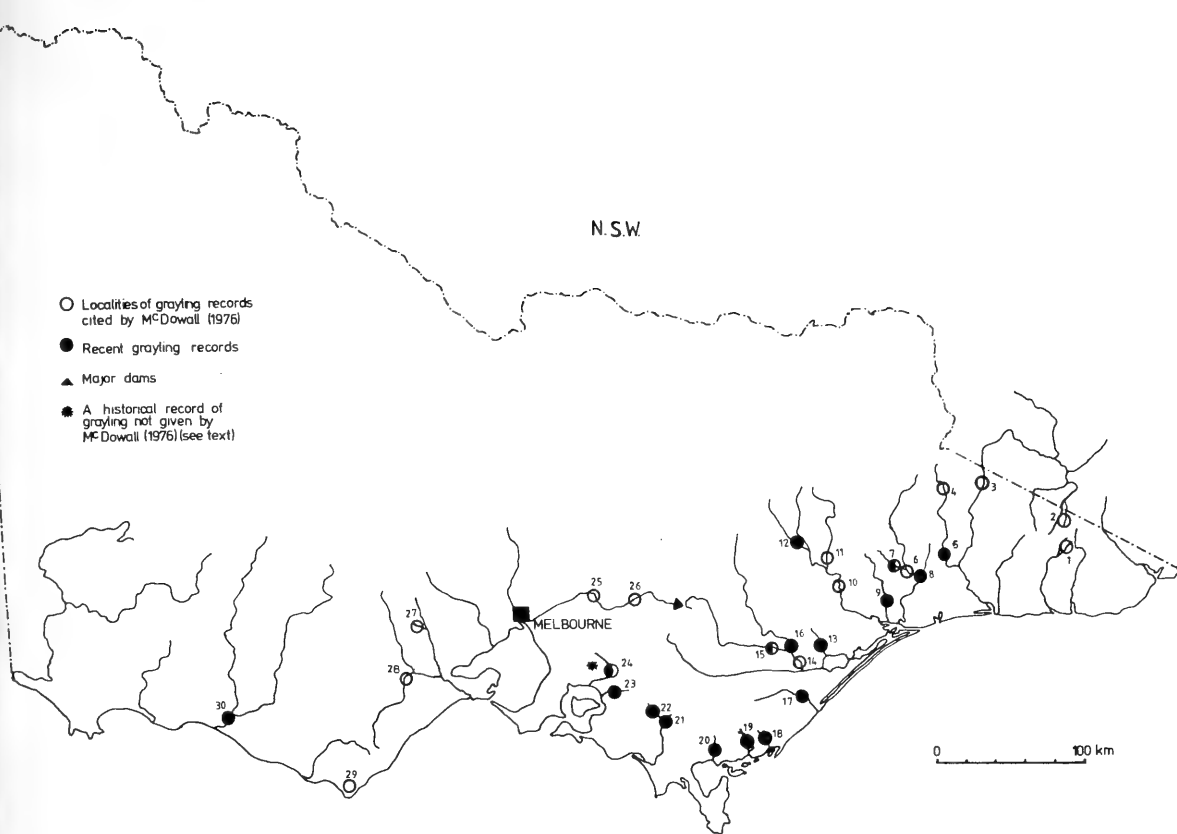


FIG. 2. Distribution of *P. maraena* in Victoria, mapped from recent records and those cited by McDowall (1976). 1. Combienbar River; 2. Craigie Bog Creek, tributary of Delegate River; 3. Snowy River; 4. Buchan River at Cave Creek; 5. Buchan River at 'Sunny Point'; 6. Tambo River; 7. Haunted Stream, tributary of Tambo River; 8. Tambo River at junction with Timbarra River; 9. Nicholson River; 10. Mitchell River; 11. Dargo River; 12. Wonnangatta River; 13. Avon River at 'Stratford'; 14. Thompson River at 'Sale'; 15. Thompson River at junction with Rainbow Creek; 16. McAlister River at junction with Thompson R.; 17. Merriman's Creek near 'Seaspray'; 18. Tarra River at 'Yarram'; 19. Albert River; 20. Agnes River; 21. West branch of Tarwin River; 22. Watkins Creek; 23. Lang Lang River; 24. Bunyip River; 25. Yarra River at junction with Watts River; 26. Upper Yarra River; 27. Tributary of Moorabool River at 'Meredith'; 28. Barwon River; 29. An unknown stream in the Otway region; 30. Hopkins River.

TABLE 3. Recent records of *P. maraena* from Tasmania (i.e. post McDowall 1976). Distances given are approximations. (E = Electrofishing; HL = Hook and line; S = Seine net)

Date	Locality	No. of Specimens	LCF range (mm)	Collection method	Collector	General Comments
13.xii.75	*Gordon R. 40 km from mouth	1	66	E	Fulton	
2.ii.76	North Esk R. at 'Corra Linn'	1	?	HL	Gelson	
16.ii.78	Arthur R. 200m from mouth	4	52-54 [†]	S	Last	**17.5°C, s = 0.2‰
20.ii.78	*Macquarie Harbour, near 'Strahan'	6	~100 [†]	S	Last	20.0°C, s = 0.8‰
25.ii.78	*Ettrick R. King Island, near mouth	5	62 [†]	S	Last	19.2°C, s = 1.0‰
15.iii.78	*Scamander R. 500 m above estuary	1	~220	E	Sloane	16.0°C
17.vii.78	Arthur R. 200m from mouth	5	78-89 [†]	S	Last	8.5°C, s = 0.9‰
20.vii.78	Arthur R. 200m from mouth	11	74-93 [†]	S	Last	8.4°C, s = 1.3‰
11.viii.78	Ettrick R., King Island, near mouth	4	118-141 [†]	S	Last	9.7°C, s = 0.7‰
15.x.78	Arthur R. 200m from mouth	2	89-92 [†]	S	Last	12.5°C, s = 1.2‰
15.x.78	Arthur R. at mouth	1	47 [†]	S	Last	13.3°C, s = 2.2‰ — specimen was not pigmented
18.x.78	*Pieman R. at the "Shacks"	4	49-51 [†]	S	Last	11.6°C, s = 1.2‰ — all specimens pigmented
6.ii.79	Douglas R. 2 km above estuary	1	92	E	Sloane	18.0°C
7.ii.79	Scamander R. 500m above estuary	4	85-207	E	Sloane	22.0°C, ripe ♂
16.ii.79	Duck R. 15 km from sea	2	122-155	E	TIFC ^a	12.0°C
28.iii.79	Scamander R. 100m above estuary	3	165-205	E	Sloane	14.5°C, ripe ♂ and ♀
29.iii.79	*Meredith R. 400m above estuary	5	87-121	E	Sloane	15.5°C

* New records for Tasmania

** Water temperatures

[†] These measurements represent standard lengths (SL) not LCF

s = Salinity in ppt

^a Tasmanian Inland Fisheries Commission

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specimen with an LCF of 216 mm caught in the North West Bay River (Fig. 3:8) on 26-11-1972 is the only additional historical record.

The collections from the Pieman (4), [McDowall (1976) mentioned only an 'unconfirmed report' from this locality], Gordon (6), Meredith (11) and Scamander (13) Rivers and Macquarie Harbour (5) represent new records (see

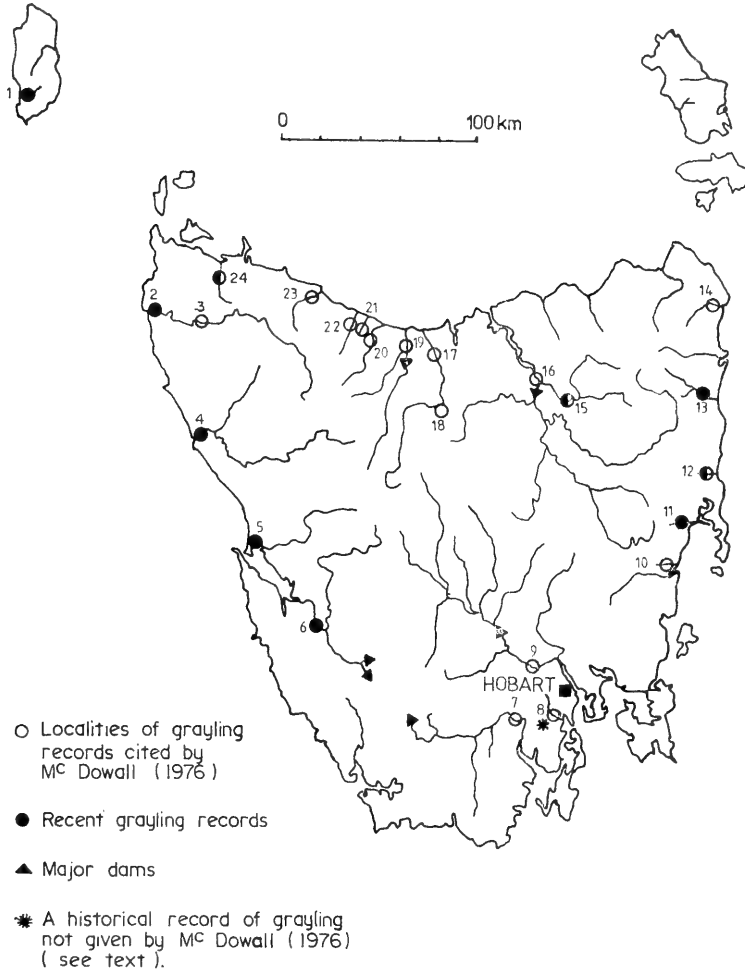


FIG. 3. Distribution of *P. maraena* in Tasmania, mapped from recent records and those cited by McDowall (1976). 1. Ettrick River, King Island; 2. Arthur River at mouth; 3. Arthur River; 4. Pieman River; 5. Macquarie Harbour, near 'Strahan'; 6. Gordon River; 7. Huon River; 8. North West Bay River; 9. Derwent River; 10. Lisdillon River; 11. Meredith River; 12. Douglas River; 13. Scamander River; 14. Ansons River; 15. North Esk River; 16. Tamar River; 17. Mersey River; 18. Coiler River at 'Kimberly'; 19. Forth River; 20. Leven River; 21. Sulphur Creek; 22. Blithe River; 23. Inglis River; 24. Duck River.

TABLE 4. Nature of sampling effort by authors in streams from which *P. maraena* has been recorded. Rank values are as follows:—
 1. Sampled infrequently for other species; 2. Sampled frequently for other species; 3. Sampled infrequently for *P. maraena*;
 4. Sampled frequently for *P. maraena*; 5. Not sampled.

NEW SOUTH WALES			VICTORIA			TASMANIA		
Locality	Fig. 1 reference	Rank	Locality	Fig. 2 reference	Rank	Locality	Fig. 3 reference	Rank
Grose R.	1	3	Combiobar R.	1	5	Etrick R.	1	1
Macquarie Rivulet	2	3	Craigie Bog Ck.	2	5	Arthur R.	2,3	1
Broughton Ck.	3	3	Snowy R.	3	5	Pieman R.	4	1
Kangaroo R.	4	1	Buchan R.	4,5	1,3	Macquarie Harbour	5	1
Shoalhaven R.	5,7	1,3	Tambo R.	6,8	1,4	Gordon R.	6	1
Yalwal Ck.	6	1	Haunted S.	7	1,3	Huon R.	7	1
Clyde R.	8	3	Nicholson R.	9	2	North West Bay R.	8	1
Buckenbowra R.	9	1	Mitchell R.	10	1	Derwent R.	9	1
Deua R.	10	5	Dargo R.	11	1	Lisdillon R.	10	5
Gulph Ck.	11	5	Wonnangatta R.	12	1	Meredith R.	11	1
Brogo R.	12	1,3	Avon R.	13	5	Douglas R.	12	1
Tantawangalo R.	13	3	Thompson R.	14,15	1,3	Scamander R.	13	1
			McAlister R.	16	5	Ansons R.	14	5
			Merriman's Ck.	17	1	North Esk R.	15	1
			Tarra R.	18	5	Tamar R.	16	5
			Albert R.	19	1	Mersey R.	17	1
			Agnes R.	20	1	Coiler R.	18	5
			Tarwin R. (west branch)	21	1	Forth R.	19	5
			Watkins Ck.	22	1	Leven R.	20	5
			Lang Lang R.	23	1	Sulphur Ck.	21	5
			Bunyip R.	24	2	Blythe R.	22	5
			Yarra R.	25,26	2	Inglis R.	23	5
			Tributary of Moorabool R.	27	5	Duck R.	24	1
			Barwon R.	28	1			
			Otway region	29	1			
			Hopkins R.	30	1			

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Fig. 3). The collection from the Ettrick River (1) is the first record of *P. maraena* from King Island.

The nature of the sampling effort in streams from which grayling have been recorded is given in Table 4.

DISCUSSION

The distribution of Australian grayling indicated by these recent records is similar to their earlier distribution given by McDowall (1976), in that *P. maraena* is still found throughout much of Tasmania and Victoria, and in south-eastern New South Wales. Differences between the present and "historical" distributions are that the northern limit of the range appears to have been reduced by approximately 160 km (Fig. 1), and the southern limit reduced by 120 km on the east coast of Tasmania (Fig. 3) while the western limit in Victoria has been extended by approximately 120 km (Fig. 2). It is also now known from King Island, approximately midway between Tasmania and Victoria and from 3 localities on the mid west coast of Tasmania (Fig. 3). Grayling were also recorded from several rivers from which they were formerly unknown but they no longer appear to be present in rivers such as the Yarra and Derwent which are within their present range. The apparent northerly and southeasterly reduction in their range and their disappearance from the Yarra and Derwent Rivers can possibly be attributed to the fact that these waters are in close proximity to major population centres. It would appear that the resulting deterioration of water quality and habitat alteration in such areas has rendered these rivers unsuitable as grayling habitat. However, it should be noted that no comprehensive sampling for grayling has been carried out in these waters (Table 4). As they have recently been recorded from the Bunyip and Lang Lang Rivers in Victoria (Table 2), which have been subjected to heavy siltation and degradation through "channelisation", it is possible that *P. maraena* are persisting in some rivers within their range which are subjected to strong human influence.

The new records of grayling in those rivers marked with an asterisk in Tables 1, 2 and 3 almost certainly result from an increase in collecting activity rather than an increase in the distribution of this species. This factor may also account for the relatively high abundances of fish in some collections (Tables 1 and 2). However, the distribution of grayling within particular river systems appears to have been adversely affected by the construction of impoundments. A striking example of this occurs within the Shoalhaven River, N.S.W., where grayling were formerly recorded from a major tributary, the Kangaroo River (McDowall 1976). Since the completion of Tallowa Dam in 1976, situated at the junction of the Shoalhaven and Kangaroo Rivers, grayling have only been recorded below this impoundment. Bishop and Bell (1978a) made a large collection of *P. maraena* below the dam shortly after its completion and expressed concern at the apparent effect the dam had had on movements of this species.

The occurrence of what appeared to be 0+ fish (see Bishop and Bell 1978b) below Tallowa Dam during December 1978 (Table 1) indicates that *P. maraena* were still reproducing within the Shoalhaven River system. However, as nothing is known on juvenile dispersal mechanisms in this species, no firm conclusions can be drawn until the reproductive cycle of this species is clearly understood.

The Gordon and Pieman Rivers in Tasmania and Merriman's Creek and Mitchell River in Victoria, in which grayling have recently been recorded, are due to be impounded in the near future. Hence it is important to determine the exact effect dams and weirs have on the movements of *P. maraena* before these dams are built.

Ripe fish collected in the Scamander River, Tasmania, during February and March 1979 (Table 3), from the Brogo River, N.S.W. during March 1980 (Table 1) and from the Tambo River in Victoria during April and early May 1979 (Table 2) are in accord with records of ripe fish given by McDowall (1976). These records confirm the ideas of Bishop and Bell (1978b) that *P. maraena* spawns in freshwater from late summer to early Autumn.

The small grayling collected at the mouth of the Arthur River and near the mouth of the Pieman River, Tasmania (Table 3) are among the smallest grayling ever collected. Their occurrence along with other relatively small grayling collected at or near the mouths of several rivers in Tasmania (see Table 3) helps to confirm the suggestion of Bishop and Bell (1978b) that *P. maraena* is "probably anadromous, with larvae drifting downstream and the juveniles returning to the rivers towards the end of their first year." It is interesting to note, however, that the salinities at these localities were very low ($0.7\text{--}2.3\text{‰}$) and therefore they do not represent typical estuarine habitats within the range of *P. maraena*. There are no authentic records of *P. maraena* from estuaries in New South Wales or Victoria.

The small specimen of *P. maraena* collected on 15-10-1978 at the mouth of the Arthur River (Table 3) was unpigmented and was in close association with a school of Tasmanian whitebait *Lovettia sealii*. Lynch (1966) also reports that juvenile grayling were taken in whitebait samples from the Blythe, Forth and Leven Rivers during spring. Thus it appears that juvenile grayling in Tasmania may at times associate with schools of *Lovettia sealii* (and possibly *Galaxias* spp.) during spring when the whitebait migrate from the sea to rivers to spawn (Blackburn 1950). Juvenile grayling collected from the Shoalhaven River and Clyde River on the 15 and 16-12-1978, respectively (Table 1), were in close association with smelt *Retropinna semoni* of approximately the same size.

Further research aimed at determining life cycle, larval dispersion mechanisms and genetic structure of the population (i.e. using morphological and electrophoretic techniques to determine whether grayling populations in Tasmania, King

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Island, Victoria and New South Wales are sustained by a single stock) is required.

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Ecological studies of *Antechinus stuartii* and *Antechinus flavipes* (Marsupialia: Dasyuridae) in open-forest and woodland habitats

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ABSTRACT

Live trapping studies of *Antechinus stuartii* and *Antechinus flavipes* were conducted in open-forest and woodland habitats near Canberra, Australian Capital Territory. Mobility of male and female *A. stuartii* was high, but densities averaged a low 1-2 individuals per hectare. *A. stuartii* captures were positively associated with gully situations and sites providing cover. *A. flavipes* captures were associated with rocky outcrops. Data are also presented on activity, reproduction and body measurements of both species.

INTRODUCTION

Marlow (1958) pointed out that the most important factor determining the distribution of marsupials in New South Wales was the nature and density of plant cover. Open-forest and woodland formations cover much of the state (Specht, 1970) and provide optimal habitat for at least twelve species of marsupial, and marginal habitat for several others (Tyndale-Biscoe and Calaby, 1975). However, little is known of the ecology and distribution of marsupials in these habitats. Information on small dasyurids is particularly lacking, and may result in part from poor trapping returns, such as 2.5% (Calaby, 1971), or from the apparent trap-shyness of certain species, such as *Sminthopsis* spp. (Archur, 1979).

This paper reports the results of mark-recapture studies carried out on *Antechinus stuartii* and *Antechinus flavipes* (Dasyuridae) in open-forest and woodland near Canberra, Australian Capital Territory, during 1978 and 1979. Particular attention is focussed on numbers and movements, habitat utilisation, reproduction, and body measurements.

MATERIALS AND METHODS

STUDY AREAS

Nineteen different localities within a 45 km radius of Canberra were sampled. These are shown in Fig. 1.

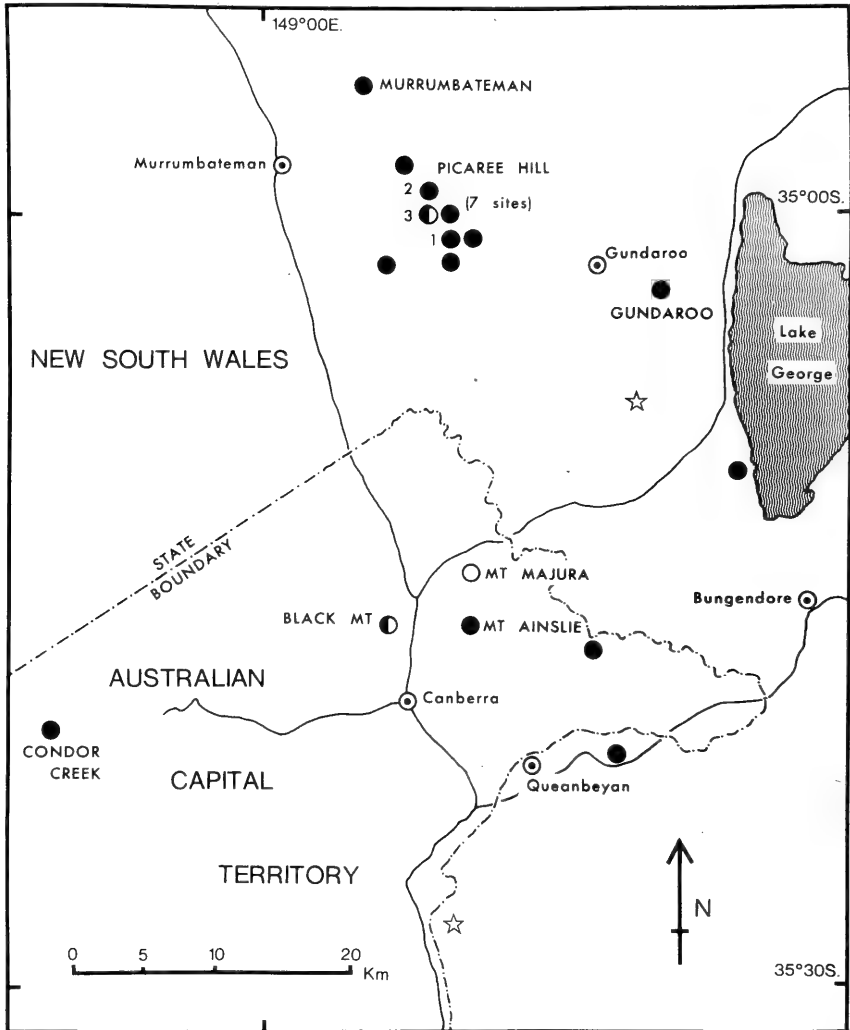


FIG. 1. Map showing the distribution of localities trapped for *Antechinus*. Solid circles, *A. stuartii* captured; open circle, *A. flavipes*; half-open circle, both species; stars, trapping unsuccessful. Localities mentioned in the text are shown in capital type.

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Vegetation was defined as open-forest when foliage cover of the tallest stratum was 30-70% and as woodland when foliage cover was 10-30% (Specht, 1970). Both vegetation types were found in varying proportions at all localities. Mean annual rainfall is about 60 cm (Bureau of Meteorology, 1968), except at Condor Creek, where rainfall exceeds 80 cm. Altitude was generally 600-800 m above sea level.

Stringybark (*Eucalyptus macrorrhyncha*) and scribbly gum (*E. rossii*) were the dominant tree species in most localities. The boxes (*E. melliodora*, *E. goniocalyx* and *E. polyanthemos*) were scattered in open-forest but predominated in open woodland areas. The wattles (*Acacia dealbata*, *A. rubida* and *A. implexa*) occasionally replaced *Eucalyptus* spp. in the canopy. Black she-oak (*Casuarina littoralis*) and cherry ballart (*Exocarpus cupressiformis*) also occurred as isolated specimens. Young or stunted *Eucalyptus* spp. and *Acacia* spp. provided sparse under-canopy cover. Ground level vegetation was usually sparse and patchy, and characteristic of thin and infertile soils (Specht, 1970). Tussocks of grass (*Danthonia pallida*) were dominant in most areas, and other grasses such as *Nasella trichotoma* and slender spear grass (*Stipa falcata*) occurred infrequently. A few small flowering shrubs (*Melicbrus urceolatus*, *Hibbertia obtusifolia*, *Brachyloma daphnoides* and *Pultanaea boormanii*) were widely distributed, but contributed little to ground cover. Blackboys (*Xanthorrhoea australis*) were found occasionally in sheltered and ungrazed sites. The vegetation of three localities (Black Mountain, Mt. Majura and Mt. Ainslie) was more complex and is described in detail by Ingwersen *et al.* (1974). Additional ground cover in all areas was provided by fallen logs and rotten stumps. Litter was thick and consisted mainly of fallen *Eucalyptus* leaves and peeled bark fragments of *E. rossii*.

No wildfires have occurred in any of the study localities for at least 8 years, and at the western most locality, Condor Creek, no major fires have been recorded since 1939 (Florence, 1973). The relationship of fire history to ground litter was not quantified, but the recent absence of wildfires has probably contributed substantially to litter build-up.

FIELD METHODS

Fieldwork began in May 1978, and continued intensively until the end of July, when all 19 localities had been sampled. Sampling continued sporadically during August and September, 1978, at Gundaroo, Picaree Hill and Mt. Majura, and also during March, July and August 1979, at various localities.

Small mammal traps (Elliott, type B, 32 x 9 x 9 cm) were used to capture *Antechinus*. Between 45 and 200 traps were laid at each locality, at 15-20 m intervals, in either grid or line formation. Traps were placed singly at each station and were provided with cotton wool bedding and a bait of honey, rolled oats, peanut butter and bacon. Traps were always cleared early in the morning (night captures) and at 7 localities a further evening trap round was carried out (day

captures). Animals were weighed, sexed and individually marked by toe-clipping. Some individuals were also lightly etherised at the time of first capture in any trapping session. Measurements were made of head-body and tail length as described in Wakefield and Warneke (1967). Reproductive condition was assessed by the development of the pouch (and pouch young) of the female, and in the male by the size and appearance of the scrotum and the development of the penis and sternal gland. This assessment was based on the detailed descriptions of the appearance and behaviour of reproductive and post-reproductive *Antechinus* provided by Marlow (1961), Woolley (1966a) and Moore (1974).

Trap stations were classified by situation and site. Four categories of situation were recognised: (i) gully, (ii) ridge, (iii) hillside, and (iv) flat forest. Seven categories of site were recognised: (i) under a log, (ii) in a log, (iii) base of a rough-barked tree, (iv) base of a smooth-barked tree, (v) open ground, (vi) under a rock, and (vii) in a tree-log complex. Any fallen tree or stump greater than 8 cm in diameter and greater than 100 cm in length was classified as a log, and any site with continuous log cover between at least two trees was classified as a tree-log complex. A χ^2 contingency table revealed no significant association between situation and site classifications ($P > 0.5$).

THEORETICAL METHODS

Grids using a minimum of 80 trap stations were set up in 5 localities in order to estimate movements and population density. Traps were cleared twice daily for 3-5 consecutive days. Population size was calculated using Hayne's (1949) modified ratio method, and density was expressed in terms of true trapping area after the addition of a boundary strip to the grid sides. The width of the boundary strip was equivalent to the average distance moved between successive captures (Av. D.) for grid individuals (Brant, 1962).

RESULTS

Antechinus stuartii was captured at 16 of the 19 localities sampled, *A. flavipes* at 3 of the 19. Sympatry was recorded at 2 localities. Two localities yielded no animals and have been omitted from further consideration. For clarity, the results for *A. stuartii* and *A. flavipes* have been considered separately.

Antechinus stuartii

TRAPPING SUCCESS

(a) Night Captures

One hundred and eighteen individuals (69 ♂, 49 ♀) were captured in 5690 trap-nights from May-July, 1978. Fifty-one individuals (29 ♂, 22 ♀) were recaptured, with a recapture frequency of 1.6 times per individual. The total number of recaptures was 91 (49 ♂, 42 ♀) and the total number of captures

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209. Average capture success for night trapping was therefore 3.67% (range 1-10%).

(b) Day Captures

Twenty-six individuals (19 ♂, 7 ♀) were captured in 2750 day-time traps. Sixteen of these had been captured previously at night, and 10 (9 ♂, 1 ♀) were captured only during day trapping. In contrast to the night-time recapture success, no individual was captured more than once during the day-time, and overall trap success was a low 0.95%. Significantly more males than females were captured by day ($P < 0.05$) in contrast to night captures, when no significant difference was found in the sex ratio ($P > 0.05$).

TABLE 1
Av. D. estimates of *A. stuartii* during 1978 and 1979.

Estimates of Av. D. (m) \pm s.d.			
Date	♂	♀	Total
May, 1978	58.7 \pm 17.9 (n=4)	30.2 \pm 9.2 (n=3)	46.5 \pm 20.5 (n=7)
June, 1978	50.5 \pm 25.4 (n=6)	49.1 (n=2)	50.1 \pm 22.0 (n=8)
July, 1978	52.5 \pm 23.0 (n=7)	48.0 \pm 11.8 (n=9)	50.0 \pm 17.2 (n=16)
August, 1978	60.7 \pm 20.0 (n=3)	27.5 \pm 19.3 (n=4)	41.7 \pm 25.2 (n=7)
March, 1979	20.0 (n=2)	22.7 \pm 4.6 (n=3)	21.6 \pm 3.6 (n=5)

MOVEMENTS AND POPULATION DENSITY

Both night and day captures contributed to the estimates of Av. D. (Table 1) and density (Table 2). Av. D. estimates were similar for males and females in all months except May and August 1978, when males appeared to be more mobile, but statistical comparisons were limited because of small sample size. The larger July sample yielded no significant difference in Av. D. between males and females ($P > 0.1$). Population density was estimated from 5 localities during the period May-July, 1978 (Table 2). True trapping areas were calculated using boundary strip widths of 50 m — approximately the total (male and female) Av. D. values for these months.

HABITAT UTILISATION

Tables 3 and 4 present data on habitat utilisation and site selection for the 209 night captures of *A. stuartii* during May-July, 1978. A simple χ^2 test was used to determine whether trapping rates departed from expected values. Essentially similar results were obtained for day captures. The most significant departure from expected ($P < 0.001$) arose from a high number of captures at tree-log complex sites, but significantly higher trapping rates were found also in gully situations ($P < 0.05$) and in logs ($P < 0.01$). Ridge situations, tree bases and open ground sites all returned significantly lower trapping rates ($P < 0.05$).

TABLE 2
Density estimates of *A. stuartii* from five open-forest habitats.

Locality and date	Number captured	Population size	Total Av. D. (m)	Actual trapping area (ha)	True trapping area (ha)	Density <i>A. stuartii</i> /ha (m)
Picaree Hill area 1. 24-28 May, 1978	14	15.6	50	5.04	9.64	1.62
Picaree Hill area 2. 26-28 May, 1978	9	10	50	2.52	5.72	1.75
Picaree Hill area 3. 15-19 June, 1978	19	20.6	50	5.76	10.76	1.91
Gundaroo 3-7 July, 1978	11	11	50	5.76	11.76	0.94
Murrumbateman 24-26 July, 1978	16	18.7	50	4.48	8.88	2.1

TABLE 3
Habitat utilisation of *A. stuartii*, night captures only.

Habitat	Trap-nights	Animals captured		X ²
		Observed	Expected	
Gully	1290	62	47.4	4.5
Ridge	467	8	17.2	4.9
Hillside	3478	122	127.7	0.3
Flat forest	455	17	16.7	0.0
Total	5690	209	209	9.7 p<0.05, 3 d.f.

WOODLAND ECOLOGY OF *ANTECHINUS*

TABLE 4

Trap-site selection of *A. stuartii*, night captures only.

Trap-site	Trap-nights	Animals captured		X ²
		Observed	Expected	
Under log	1887	76	69.3	0.6
In log	413	27	15.2	9.2
Rough-barked tree base	863	20	31.7	4.3
Smooth-barked tree base	1196	27	43.9	6.6
Open ground	552	11	20.3	4.3
Under rock	109	3	4.0	0.3
Tree-log complex	670	45	24.6	16.9
Total	5680	209	209	42.2 p<0.001, 6 d.f.

TABLE 5

Body measurements of *A. stuartii* and *A. flavipes*, July 1978 and July 1979.

Species	Mean body wt (g) \pm s.d.	Mean head-body length (mm) \pm s.d.	Mean tail length (mm) \pm s.d.
<i>A. stuartii</i> ♂	28.3 \pm 3.2 (n=27)	99.3 \pm 5.9 (n=15)	84.0 \pm 3.7 (n=15)
♀	21.6 \pm 2.5 (n=21)	91.5 \pm 4.2 (n=12)	78.1 \pm 6.2 (n=12)
<i>A. flavipes</i> * ♂	51.2 \pm 5.7 (n= 9)	124.9 \pm 8.6 (n= 9)	95.6 \pm 8.4 (n= 9)
♀	34.8 \pm 3.2 (n= 8)	105.1 \pm 7.8 (n= 8)	81.0 \pm 3.7 (n= 8)

* Includes data supplied by K. Kukolik (see text).

BODY WEIGHTS AND MEASUREMENTS

Body weight and head-body and tail measurements from July captures are presented in Table 5. Sexual dimorphism is evident from all measurements: males are significantly heavier ($P<0.001$) and significantly longer in both head-body ($P<0.001$) and tail ($P<0.01$) than females. Significant size differences were found in all sample months except March, 1979, when a small sample size and the presence of a parous female may have biased the results.

REPRODUCTION

Precise timing of field matings and parturitions was determined at selected localities during August and September, 1978, and during July and August, 1979. Trapping was conducted for 1-2 day periods at intervals of 7-12 days in each locality. At Picaree Hill, mating occurred during the first two weeks of August. No males were captured after 24 August, and most parturitions occurred in early September. At Gundaroo, the breeding season occurred about one week later. No males were captured after 29 August and a single female removed to the laboratory in late August gave birth on 20 September. The pouches of 17 females were examined during the two winter periods. All females had 5 pairs of nipples, and 6 animals carrying pouch young had a full complement of 10.

Antechinus flavipes

TRAPPING SUCCESS

Antechinus flavipes was captured at 3 localities, Black Mountain, Mt Majura and on one property at Picaree Hill. Since most captures occurred at Mt Majura, only the data obtained from this locality are presented.

Between 6 and 10 July 1978, 9 *A. flavipes* (6 ♂, 3 ♀) were captured a total of 24 times (18 ♂, 6 ♀) with a recapture frequency of 1.4 times per individual. Three of the 18 males were captured in 560 day-time traps (0.5%) while average capture success for night trapping was 2.5%.

Trapping success on Mt Majura was too low to allow estimation of movements or density, though some relevant information on habitat utilisation and body measurements is presented.

HABITAT UTILISATION

A comparison of trapping rates in gully and hillside situated traps is given in Table 6, and Table 7 compares captures of *A. flavipes* under rocks with captures at all other sites combined. Night and day captures are pooled in both analyses.

TABLE 6
Habitat utilisation of *A. flavipes*, all captures, Mt. Majura.

Habitat	Trap-nights	Animals Captured		X ²
		Observed	Expected	
Gully	238	5	4.1	0.2
Hillside	1172	19	19.9	0.04
Total	1410	24	24	0.24 p>0.5, 1 d.f.

WOODLAND ECOLOGY OF *ANTECHINUS*

TABLE 7

Trap-site selection of *A. flavipes*, all captures, Mt. Majura.

Trap-site	Trap-nights	Animals captured		χ^2
		Observed	Expected	
Under rock	173	8	3	1.2
All categories	1237	16	21	8.7
Total	1410	24	24	9.9
				$p < 0.01$, 1 d.f.

BODY WEIGHTS AND MEASUREMENTS

Body measurement data are presented in Table 5. As in *A. stuartii* sexual dimorphism is evident, males being heavier and longer than females ($P < 0.001$ for all measurements). The sample size obtained in this study was small, and data kindly supplied by K. Kukolik (pers. comm.) from adult *A. flavipes* captured on Mt. Majura and Black Mountain are also included in Table 5.

REPRODUCTION

On 4 August, 1978, two male *A. flavipes* captured on Mt. Majura had balding scrota, and one had a partially occluded eye and a recent gash on the tip of the nose. No males were captured after the first week of August, suggesting that mating may have occurred towards the end of July. A single female was captured in early September, 1978, carrying young in the pouch. Mean crown-rump length of the young was 7 mm, corresponding to an age from birth of about one week (pers. obs.). Assuming a gestation period of 25 days (Woolley 1966a, b), the time of mating would have been 30 July. Similar observations have been made by K. Kukolik (pers. comm.) on the Mt. Majura and Black Mountain populations in preceding years.

Mating occurred later in the *A. flavipes* population at Picaree Hill. On 20 August, 1979, 3 females and 1 male were captured. From the condition of the pouches and surrounding hairs, the females appeared to be in oestrus. The male had a shrunken, bald, blue-pigmented scrotum and appeared weak. These observations suggested that mating had occurred around mid-August, 3 weeks later than at Mt. Majura.

All 8 females examined had 12 nipples, and one individual with young had a full pouch of 12.

DISCUSSION

TRAPPING SUCCESS AND POPULATION ESTIMATES

A. stuartii is widespread, though never abundant, in open-forest and woodland habitats near Canberra. The maximum densities of 1-2 individuals per hectare indicated by this study do not approach the maximum density of 24.9 per hectare calculated by Fleming (1975) from the data of Wood (1970), nor the 18 per hectare of Hall (pers. comm.) in Nagy *et al.* (1978). The values are closer to the estimates of 2.2-3.45 per hectare obtained by Barnett *et al.* (1977) from tall open-forest and rainforest, and similar to Fletcher's (1977) estimate of 1.9 per hectare from dry sclerophyll forest. Had the estimates of the present study been calculated by direct enumeration over unadjusted trapping areas, close approximation with the findings of the latter studies would have been obtained.

Population size and recapture success appear to be stable until the post-mating die-off of males. An average recapture rate of 0.44 was recorded for the May-July 1978 period, with some individuals being recaptured 5-6 times. The recapture rate of female *A. stuartii* fell to 0.3 per trapping session following mating and when young were in the pouch. Length of individual trapping periods certainly affected recapture success. New individuals continued to be captured up to the third and perhaps fourth days of any trapping session, but few new individuals appeared on the fifth day. Average recapture success would probably have increased had a uniform 5-6 day trapping regime been employed.

A. flavipes occurs on the ecological "islands" of Black Mountain and Mt. Majura, and alongside *A. stuartii* in open-forest at Picaree Hill. Trapping success for *A. flavipes* was always low, suggesting that it successfully exists at lower densities than *A. stuartii*. Reeckman (1975) surveyed many populations of *A. flavipes* in parts of Victoria, and calculated a maximum density of 4.17 individuals per hectare (unadjusted for true trapping area) at the most productive site. A denser population of *A. flavipes* may exist near Wagga Wagga, N.S.W., but no explicit estimates are available (B. Gall, pers. comm.).

Both *A. stuartii* and *A. flavipes* were captured more frequently by night than by day. Similar activity patterns have been observed by Wood (1970) and Warden and Wallis (1979) for *A. stuartii*, though Dwyer *et al.* (1979) recorded extensive day-time activity for *A. flavipes* in Queensland. Male *A. stuartii* (and possibly male *A. flavipes*) were captured more frequently than females by day, reflecting a greater level of day-time activity among males.

MOVEMENTS

Av. D. values for *A. stuartii* were calculated from captures made on 20 m grids in all months except June 1978, when a 15 m grid was used. Though trap spacing is known to affect estimates of Av. D. (Brant, 1962), June estimates were not very different from estimates obtained in May and July. Av. D. values

for both males and females appeared similar for much of the year, though some increase was recorded among males as mating approached in August.

The values of Av. D. obtained for *A. stuartii* in this study generally exceed those obtained by other workers. Wood (1970) obtained values of about 20 m for females and 30 m for males during May-August, while Braithwaite (1973) recorded values of about 20 m for males and 21 m for females. Both of these studies were carried out in subtropical rainforest. The differences in Av. D. probably reflect differences in habitat productivity: animals inhabiting relatively unproductive dry woodland must forage further to acquire the same amount of trophic energy than animals in productive rainforest. Morton (1978) linked the large dispersion and movement patterns of *Sminthopsis crassicaudata* in grassland habitat to the distribution of invertebrate food.

HABITAT UTILISATION

Previous studies on habitat utilisation of *A. stuartii* have generally found no correlation between site captured and habitat structure (Braithwaite, 1973; Press, 1976; Fletcher, 1977) though Barnett *et al.* (1978) found *A. stuartii* to be significantly associated with logs. Stewart (1979) attributed a lack of correlation to measurement of inappropriate habitat variables. In a relatively unstructured environment, *A. stuartii* appears to use whatever cover is available. Hence, in dry open-forest and woodland, it tends to be found in sheltered gully situations, and in strong association with specific features providing maximum cover (see Table 4, compare observed and expected captures of *A. stuartii* in logs and in tree-log complexes with captures in open sites and open tree base sites). Many *A. stuartii* were also captured in woodland bordering pastures or open sites. The presence of scarab larvae in some scats suggested that foraging sometimes occurred in open grassland.

A. flavipes is associated with rocky sites (see Table 7). A similar situation occurs in the Grampians (Reeckman, 1975) where most *A. flavipes* were captured near rocks on a steep sandstone hillside. These findings and the observations of Fleay (1949, 1950) suggest that rock crannies may provide nesting sites for *A. flavipes*.

Insufficient captures were made at localities where *A. stuartii* and *A. flavipes* were sympatric to quantify differences in their habitat utilisation.

BODY MEASUREMENTS

Both sexes of *A. flavipes* are heavier and have a greater head-body length than either sex of *A. stuartii* ($P < 0.001$) for July data. Similar differences in size were documented by Wakefield and Warneke (1967), suggesting that *A. flavipes* is consistently the larger species. Body size differences may facilitate coexistence among similar congeneric species by permitting differential resource utilisation

(Hutchinson, 1959, Wilson, 1975). Since neither Woolley (1966a) nor the present study were able to detect major differences in habitat utilisation between sympatric *A. stuartii* and *A. flavipes*, body size may be a significant niche dimension.

Sexual dimorphism was very marked in both species and has been reported previously (e.g. Horner and Taylor, 1959). Intersexual size differences may increase niche width (Clutton-Brock and Harvey, 1978). The larger size of male *Antechinus* may also maximise their reproductive success (Braithwaite, 1973).

REPRODUCTION

Reproductive events in both species appeared to take place at different times in different localities. Mating of *A. stuartii* generally occurred in August, while *A. flavipes* on Mt. Majura and Black Mountain appeared to mate earlier, in late July. *A. flavipes* at Picaree Hill mated later than most *A. stuartii* populations sampled, and later than *A. flavipes* on Mt. Majura. Woolley (1966b) found that *A. flavipes* collected at Picaree Hill mated 2-3 weeks earlier than *A. stuartii*, when both were kept under laboratory conditions. The discrepancy above is difficult to explain, since timing of reproductive events is usually synchronous within a population from year to year (Wood, 1970). Woolley (1966a, b) considered that interspecific differences in the time of mating could reproductively isolate sympatric species. Conceivably too, by mating earlier, *A. flavipes* could maintain a growth advantage over *A. stuartii*, thus maximising body size differences. Precise timing of field matings and more intensive survey methods are required to clarify both reproductive and ecological relationships between these two species.

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Acclimation of CTM, LD₅₀, and Rapid Loss of Acclimation of Thermal Preferendum in Tadpoles of *Limnodynastes peronii* (Anura, Myobatrachidae)

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ABSTRACT

Groups of tadpoles of *Limnodynastes peronii* (Anura, Myobatrachidae) were kept at two temperatures (15° and 25°C) for 45-105 days. In a thermal gradient (6-36°C), initial thermal preferenda were significantly different in 15° and 25°C history groups, approximately 13° and 21°C respectively. However, after 2.5 hours these initial differences were no longer seen and the final thermal preferendum was approximately 18°C regardless of previous thermal history. Critical thermal maxima and LD₅₀ increased following warm thermal history. Considering these results and the lack of metabolic acclimation reported elsewhere, these tadpoles can be seen as ectotherms whose thermal strategies are behavioural rather than physiological or biochemical. The rapid loss of acclimation of preferred temperature is discussed in relation to Fry's "final preferendum" paradigm.

INTRODUCTION

Tadpoles of *Limnodynastes peronii* show no evidence of thermal metabolic acclimation when kept at 15°C and 25°C for period of 45-75 days (Marshall and Grigg, 1979). This suggests that the major thermally significant strategies in these tadpoles may be behavioural rather than biochemical or physiological, and leads to questions about the ability of tadpoles of *L. peronii* to select a preferred temperature within the habitat.

Field observations on other species suggest that tadpoles seek out suitable thermal environments (Brattstrom, 1963). Lucas and Reynolds (1967) examined the behaviour of tadpoles of *Rana pipiens* and *Rana catesbeiana* in a thermal gradient. They found that tadpoles of both species aggregated at specific temperatures within the gradient and that the preferred temperature was influenced by previous thermal history. The main aims of this study were to determine the extent to which tadpoles of *L. peronii* aggregate within a thermal gradient and whether or not any thermal preference is affected by previous thermal history.

Many studies of Amphibia have emphasised the dependence of various physiological parameters upon previous thermal history. Brown (1969) showed that

heat resistance of four species of tadpoles could be increased by previous exposure to warm temperatures. Rapid thermal acclimation of CTM (critical thermal maximum), thermal LD₅₀ and OS (onset of spasms) temperatures have been demonstrated in many Amphibia (Brattstrom and Regal, 1965; Brattstrom, 1968, 1970; Holzman and McManus, 1973). Accordingly, further aims of the study were to determine the effects of thermal history on thermal LD₅₀ and CTM.

MATERIAL AND METHODS

L. peronii is a large (to 65 mm total length) widespread myobatrachid frog which occurs on the coastal plains and in the ranges of eastern Australia. In suburban areas it frequently makes use of artificial ponds for breeding and seems tolerant of polluted water (Barker and Grigg, 1977). Its distribution from 18-42°S latitude suggests that it is eurythermal. The tadpoles are long-lived, often overwintering (Barker, pers. comm.).

Egg masses of *L. peronii* were collected from the Sydney suburb of Sylvania, transported to the laboratory in water from the site of collection, and kept at room temperature (ca. 20°C) until hatching. Groups of tadpoles were then subjected to short-term (45-60 days) and long-term (90-105 days) exposures to warm (25°C) and cool (15°C) temperatures. Tadpoles were fed frozen lettuce every second day and the water was replaced weekly with fresh water at the required temperature. Tadpoles were kept in constant temperature rooms under constant illumination. Measurements of PBT (preferred body temperature), LD₅₀ or CTM were made on 15° and 25°C tadpoles alternately to minimise any likelihood of a time-bias being introduced.

(a) CRITICAL THERMAL MAXIMUM

CTM was determined for 30 tadpoles from each of the four experimental groups, using the method described by Hutchison (1961).

(b) THERMAL LD₅₀ DETERMINATION

Only tadpoles exposed to constant temperatures for 90-105 days were used for this measurement.

Preliminary experiments indicated that LD₅₀ for cold-history and warm-history tadpoles would be within the ranges 34-36°C and 35-37°C respectively. Accordingly, water baths were set up at 34, 35, 36 and 37°C ($\pm 0.1^\circ\text{C}$). Thirty, 60 and 30 cold-history tadpoles were placed in water baths at 34, 35 and 36°C ($\pm 0.1^\circ\text{C}$) respectively and the number of tadpoles surviving 24 hours was recorded. Thirty, 60 and 30 warm-history tadpoles were tested at 35, 36 and 37°C respectively. LD₅₀ was determined by Probit analysis.

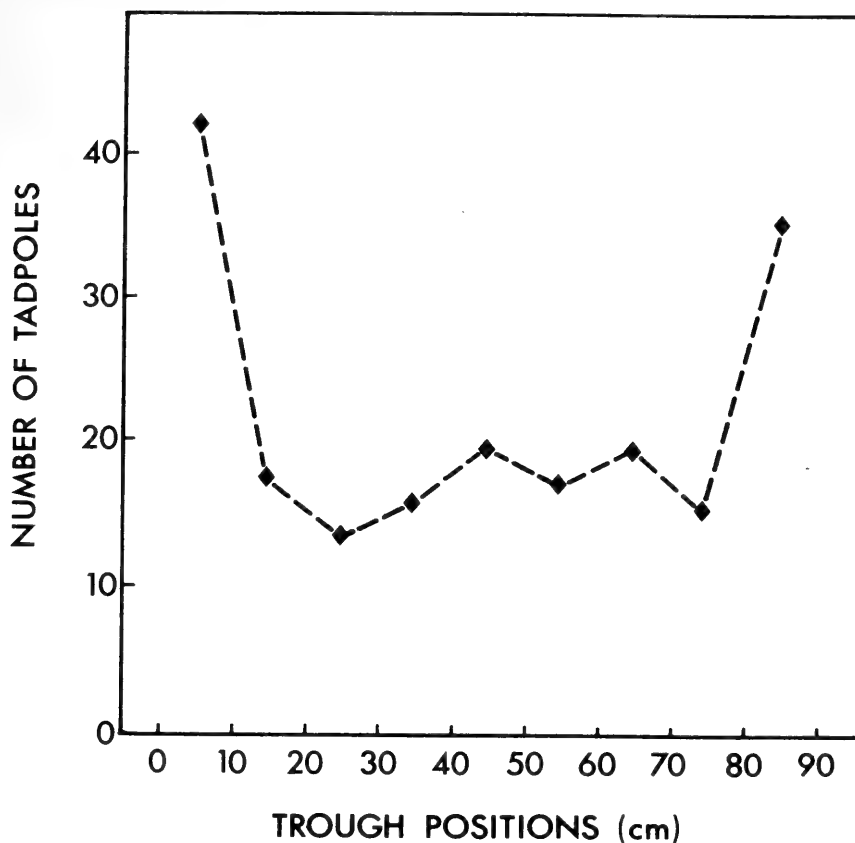


FIG. 1. Distribution of tadpoles in the trough at uniform temperature (20°C). Each point represents the cumulative number of tadpoles found at given positions over a succession of six 10-minute intervals.

(c) THERMAL PREFERENDA

Thermal preferendum was determined in a simple (6-36°C) thermal gradient, similar to that described by Lucas and Reynolds (1967). We found, as they did, that when no gradient was present tadpoles favoured the ends rather than the middle regions of the apparatus (Fig. 1). This suggests that any aggregation towards the centre of the thermal gradient, when established, indicates a response to temperature rather than to some other characteristic of the trough. Tadpoles of *L. peronii* are not known to school.

In each experiment, 30 tadpoles were introduced to the middle of the gradient (about 20°C) and their positions and corresponding temperatures were noted each 10 minutes for 2.5 hours.

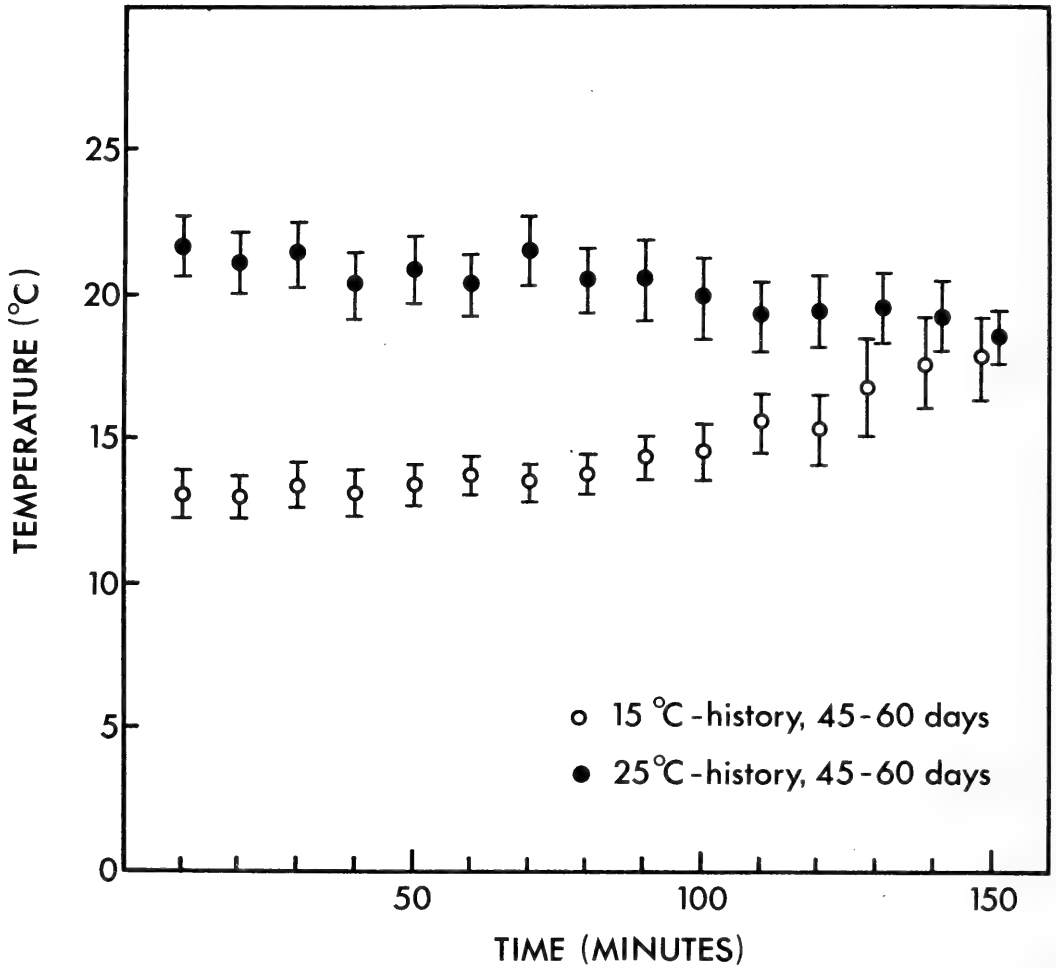


FIG. 2. Changes in thermal preferenda of two groups of tadpoles reared at 15°C and 25°C for 45-60 days. Vertical bars represent the 95% confidence limits about the mean. No measurements were made beyond 150 minutes.

RESULTS

Tadpoles with warm histories had significantly higher CTM and LD₅₀ than those with cold histories ($P < 0.005$, by Analysis and Variance) (Table 1). There were no significant differences between short-term and long-term tadpoles at either 15°C or 25°C.

TABLE 1. Critical thermal maximum (CTM) and thermal LD₅₀ in four experimental groups of thirty tadpoles.

Previous Thermal History	CTM (°C ± S.E.)	LD ₅₀ (°C ± S.E.)
Short-term, 15°C (45-60 days)	37.5° ± 0.06	—
Short-term, 25°C (45-60 days)	39.3° ± 0.04	—
Long-term, 15°C (90-105 days)	36.8° ± 0.05	34.9 ± 0.05
Long-term, 25°C (90-105 days)	39.3° ± 0.05	36.9° ± 0.07

TABLE 2. Thermal preferenda of four experimental groups of thirty tadpoles, 10 minutes after being placed in a 6-36°C thermal gradient.

Exposure Time	Preferred Temperature (°C ± S.E.)	
	15°C Thermal History	25°C Thermal History
Short-term (45-60 days)	13.2° ± 0.41 (range 8-17°)	21.5° ± 0.53 (range 17-27°)
Long-term (90-105 days)	12.5 ± 0.26 (range 10-15°)	21.8 ± 0.47 (range 18-26°)

In both short-term and long-term groups, thermal preferenda of 15°C history and 25°C history tadpoles were significantly different ($P < 0.005$), warm history tadpoles having a higher preferred temperature (Table 2).

In every case, the thermal preferenda of tadpoles changed significantly between the first and last 10 minute period ($P < 0.005$). (Figs, 2, 3).

No significant differences were found between final thermal preferenda of any of the groups (Table 3) and no seasonal trends were seen in either initial or final preferenda during the period over which experiments were carried out.

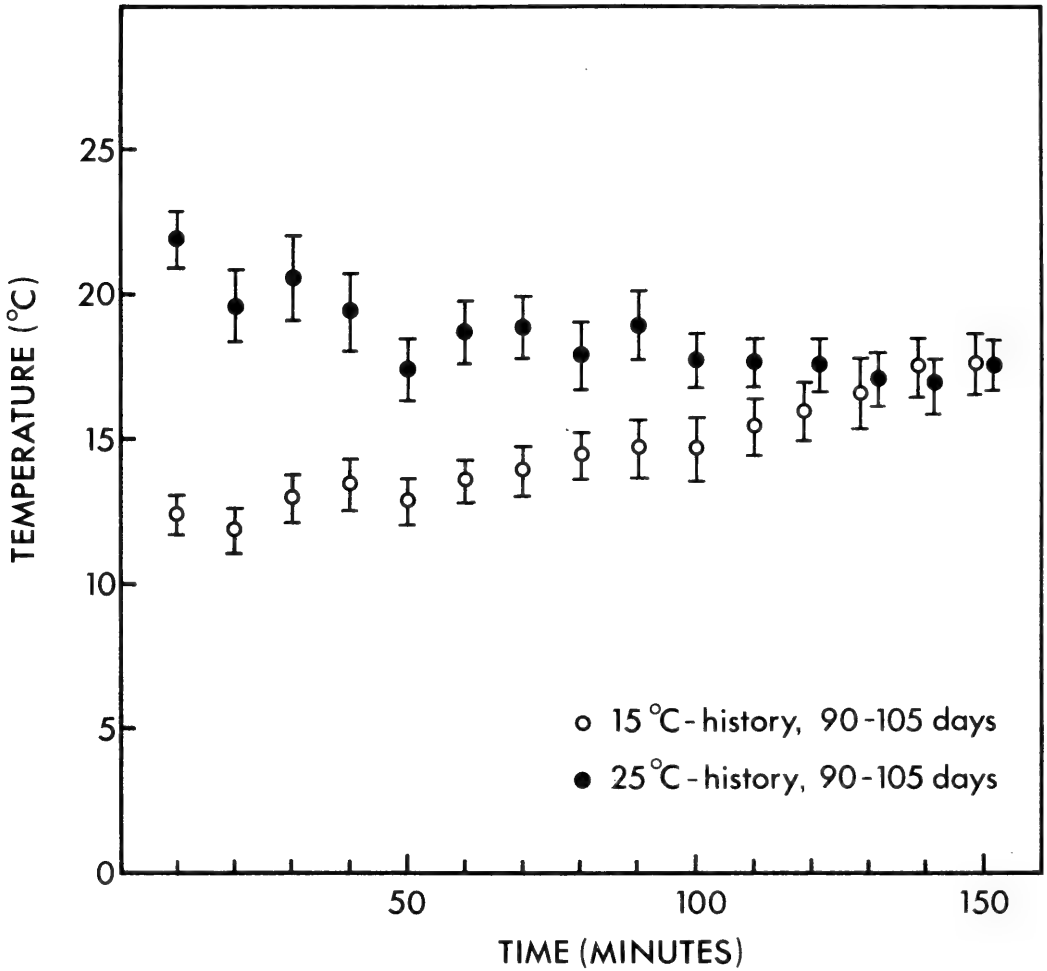


FIG. 3. Changes in thermal preferenda of two groups of tadpoles reared at 15°C and 25°C for 90-105 days. Vertical bars represent the 95% confidence limits about the mean. No measurements were made beyond 150 minutes.

CTM, LD₅₀, AND THERMAL PREFERENDUM IN A TADPOLE

TABLE 3. Thermal preferenda of four groups of tadpoles, 2.5 hours after being placed in a 6-36°C thermal gradient.

Exposure time	Preferred Temperature (°C ± S.E.)	
	15°C Thermal History	25°C Thermal History
Short-term (45-60 days)	17.9° ± 0.74 (range 8-28°C)	18.4° ± 0.58 (range 13-23°)
Long-term (90-105 days)	17.7° ± 0.53 (range 11-22°)	17.8° ± 0.40 (range 14-21°)

DISCUSSION

Both CTM and thermal LD₅₀ of tadpoles of *L. peronii* are dependant upon previous thermal history, heat resistance being increased by warm thermal history. This seems to be typical for Amphibia (Brattstrom and Regal, 1965; Brattstrom, 1968, 1970; Holzman and McManus, 1973; Brown, 1969). The results for thermal preferenda are more interesting and warrant further comment.

At a uniform temperature, tadpoles showed a preference for the ends of the test-trough (Fig. 1), in striking contrast to their aggregation at specific temperatures when a thermal gradient was established within the trough (Tables 2, 3, Figs. 2, 3). This shows that the tadpoles of *L. peronii* have a well developed ability to adjust their body temperature by selecting an appropriate water temperature. This finding is in agreement with that of Lucas and Reynolds (1967) who found that tadpoles of *R. pipiens* and *R. catesbeiana* aggregated at specific temperatures within a thermal gradient.

The effect of previous thermal history on preferred temperature (Table 2) is so transient; however, being lost after only 2.5 hours in the gradient (Table 3) that it is very difficult to ascribe any functional significance. One is led to the conclusion that tadpoles of *L. peronii* at this latitude and for at least this part of the year have a preferred body temperature of about 18°C regardless of previous thermal history. In fact, 95% of all tadpoles tested in the gradient selected temperatures between 13 and 22°C within 2.5 hours. It is difficult to compare our results with those of Lucas and Reynolds (1967) because their method of data calculation and presentation neglected the possibility of thermal preferenda changing with time while in the gradient.

Licht and Brown (1967) found similar results in the Red Bellied Newt, *Taricha rivularis*, where initial differences in preferred temperatures of newts acclimated at 5°C compared with groups acclimated at 15°C and 23°C disappeared, suggesting a final thermal preferendum of 22-24°C.

Reynolds and Casterlin (1979) have called for wider attention to be given to Fry's (1947) "final preferendum" paradigm. Briefly the "final preferendum" is the temperature to which an ectotherm in a thermal gradient will gravitate regardless of its prior thermal experience. This concept distinguishes an "acute thermal preferendum", (measured shortly after introduction to the gradient), which may be influenced by previous thermal history, and a "final thermal preferendum" which is essentially independent of prior thermal history because re-acclimation occurs during the gravitation process. The time course for reaching a final thermal preferendum is normally some days in fishes (Fry, 1947) and presumably relates to the fish's state of metabolic acclimation. The lack of thermal metabolic acclimation in tadpoles of *L. peronii* (Marshall and Grigg, 1979) may account for the rapidity with which a final preferendum is reached.

A thermal preferendum of about 18°C, as found in *L. peronii* may seem surprisingly low at times of the year when temperatures of 25°C or more can easily be encountered. One becomes accustomed to the idea that behavioural strategies of many ectotherms are directed towards the maintenance of a relatively high body temperature (which in this case would result in decreased development time). The low preferendum of *L. peronii* tadpoles shows that such a view is simplistic. It would be very interesting to see whether or not the thermal preferendum of this tadpole varies throughout its wide latitudinal range and to examine the temperature-sensitivities of their enzyme systems. Also, the preferred temperature under field conditions is unknown.

In summary, tadpoles of *L. peronii* show only minimal physiological and biochemical acclimation to high or low temperature. Whereas they exhibit an increase in heat resistance (CTM and LD₅₀) when kept at warmer temperatures, they are unable to undergo thermal metabolic acclimation (Marshall and Grigg, 1979) and show only a transient effect of acclimation temperature on thermal preferendum. Their behaviour in a thermal gradient coupled with only very limited physiological and biochemical flexibility supports the view that behaviour may be the main mechanism by which tadpoles of *L. peronii* could minimise the effects of fluctuations in environmental temperature.

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Biology of a laboratory colony of *Dasyuroides byrnei* (Marsupialia: Dasyuridae)

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ABSTRACT

Breeding and life history data obtained from a captive colony of the dasyurid marsupial *Dasyuroides byrnei* over an eight-year period are presented. Mating occurred only between April and December, with 75% of all matings recorded in May, June and July. Females experienced up to four oestrous periods during each breeding season, but many oestrous periods were not followed by pouch development. Evidence that the presence of males influenced the occurrence of pouch development and modified oestrous cycles is discussed. First pairings of both sexes were more successful than subsequent ones. Forty-one per cent of all pairings resulted in mating, but of the 84 litters born, only 51 (61%) survived to weaning. Most losses were due to litters being cannibalised by their mothers. The "critical period" for this was at 50 to 60 days of age. Causes of death and injury among laboratory *D. byrnei* are documented. Toxoplasmosis was the major disease problem detected.

INTRODUCTION

Dasyuroides byrnei is an insectivorous and carnivorous marsupial which inhabits stony desert regions of south-western Queensland and adjacent parts of north-eastern South Australia. Body weight averages 110g, and combined head and body length 170mm. Captive colonies of the species have been maintained by a number of institutions (Mack, 1961; Woolley, 1971; Collins, 1973; Aslin, 1974).

Little is known of the biology of the species in the wild. Pregnant females or females with pouch-young have been collected from the wild in June and November. Pregnant females collected in November 1968 appeared from the condition of their pouches to have already suckled one litter during 1968 (Woolley, 1971). Thus litters are born in the wild at least between June and November.

Woolley (1971) found that females in the LaTrobe University colony bred between April and December, with each female having up to three oestrous periods per year. Using the technique developed by Godfrey (1969a, 1969b, 1975), oestrus was detected by the appearance of epithelial cells in the female's urine and by a marked increase in body weight. According to Woolley (1971) in *D. byrnei* pouch

development occurred after oestrus in both mated and unmated females. The gestation period was 30 to 35 days, and therefore maximum pouch development was expected at about 35 days after oestrus.

Developmental stages of *D. byrnei* have been listed by Collins (1973) and Aslin (1974). The young are permanently attached to the female's teats until 56 days old, their eyes open at about 75 days and they are usually weaned by 100 days.

Attwood *et al.* (1975) have reported on the prevalence and clinical signs of *Toxoplasma gondii* infection in both captive and wild-caught *D. byrnei*, and Attwood and Woolley (1973, 1974), on malignant neoplasms and arachnoid villi in *D. byrnei* and other dasyurids.

This paper reports the results of maintenance of a laboratory colony of *D. byrnei* at the Institute of Medical and Veterinary Science between May 1971 and December 1978, outlining the husbandry procedures used, breeding and life history data obtained, and disease problems encountered.

MATERIALS AND METHODS

FOUNDING STOCK

The main founding stock for the I.M.V.S. colony consisted of seven females and five males captured on Coorabulka Station, Queensland, in June 1971. Five of the seven females were carrying litters of five or six new-born young when captured. From these litters the females reared 22 young to weaning age in captivity. These, together with the wild-caught adults, formed the basis of the laboratory colony. In addition, two captive-bred animals were obtained from Taronga Zoo in 1971, and two further wild-caught animals from Cordillo Downs, South Australia, in 1973. No other introductions have been made.

HOUSING

The animals were housed in a variety of rooms and cages during the history of the colony. All rooms were air-conditioned, with temperatures generally maintained between 15-25°C. Both natural and artificial lighting were used, but light cycles always approximated those of the prevailing season in Adelaide, South Australia.

The present colony is housed in three types of cages:

a. "Singles" cages which measure 230 x 500 x 700 mm and have base and three sides of particle board, with the front and hinged lid of bird-wire on a wooden frame.

b. "Doubles" cages measuring 400 x 700 x 950 mm base and three sides of wood, glass-fronted, with hinged lid of fly-wire on a wooden frame.

c. "Pens" measuring 350 x 750 x 1000 mm of particle board with bird-wire lids on wooden frames. Each pen is bottomless and has a removable door at one end, allowing adjacent pens to be joined.

Sawdust or sand is used as a substrate in cages, wooden or cardboard boxes are provided for cover, and shredded paper or straw as nesting material.

DIET

Diet varied during the seven-year period, initially being based on raw minced beef or mutton, mealworms and commercial pet-foods. In 1975, diets were modified by cooking the meat, and later cooked minced chicken was included in place of mealworms, as the supply of these became inadequate. Following analysis of dietary components in 1976, which showed that the chicken had a very high fat content, a diet of the following kind was adopted:

Monday	— Chopped hard-boiled eggs mixed with "brains and vegetables" canned baby food (Heinz)
Tuesday	— "Specific-pathogen-free" mice (from the I.M.V.S. colony)
Wednesday	— Puppy chow "Sargeant Barka complete dog food" — (William Charlick Ltd.), moistened with hot water and mixed with "brains and vegetables" baby food
Thursday	— "Specific-pathogen-free" mice
Friday	— Cooked minced beef mixed with "high-protein baby cereal" (Heinz)
Saturday	— As for Friday

The animals were fed six days a week, usually in the afternoon. About 20 grams of food was supplied per animal daily, placed in small plastic dishes which were removed and washed after each use. The "specific-pathogen-free" mice were killed and cut in halves. Each *D. byrnei* was given half a mouse per feeding.

Tap water was supplied in 300 ml glass bottles fitted with rubber stoppers and stainless steel drinking tubes which protruded through holes in the lids of the animals' cages. Each water bottle was cleaned and refilled weekly.

HUSBANDRY PROCEDURES

Newly weaned young were usually separated into same-sex litter-mate groups, and were not caged with an animal of the opposite sex until the year after their birth. Animals selected for breeding were usually first caged together in April or May of each year although some pairs were established at other times (see Table 1). A small number of pairs were maintained during the period December to April. A single male was caged with each female, and both were usually introduced simultaneously into a freshly-prepared cage. This procedure is referred to as "pairing". In some cases two pens which could be joined through removable doors were used, and the male and female were allowed to establish themselves in each pen for up

to a week before the pens were joined. Females caged with males were caught and their pouches examined weekly. The male was removed after mating was observed or after the female was found to have pouch-young. Many *D. byrnei* mated during the day, and as mating was prolonged and accompanied by noisy vocalisations, many (but not all) matings were seen. Females seen mating were left undisturbed until 36 days had elapsed since mating, then a check for young was made. No way of determining whether or not a female is pregnant has been discovered, and as births were not seen nor remains of newborn young found, females which lost young at birth could not be distinguished from those whose matings were infertile.

Females with young were left undisturbed except for daily visual checks of the mother's health and sporadic checks that young were still present. Wherever possible this was done without catching the female, by merely encouraging her to stand in such a way that the pouch area was visible. Females which lost their litters before weaning and those whose young had been newly weaned were regularly re-caged with males.

The recurrence of oestrus was followed in 30 females between April and December 1978 by means of thrice-weekly cloacal smears, which were taken by pressing the female's cloacal area briefly against a clean glass slide, avoiding contamination by faeces. (This method was used instead of urine examination as many females failed to urinate when caught.) Each smear was air-dried, stained with methylene blue and examined under a binocular microscope. The relative proportion of cornified epithelial cells to nucleated epithelial cells and leukocytes was estimated for each slide.

Smears were taken from three groups:

(1) 10 females each paired with a male. Smears were taken from these females beginning on 18 April 1978. Smearing was stopped if the female gave birth, but otherwise was continued until 22 December 1978.

(2) 10 females caged individually but with males in close proximity (in the same room). Smears were taken from 18 April to 22 December 1978.

(3) 10 females caged individually in a room which housed only other females, thereby being completely isolated from the influence of males. Smears were taken from this group between 18 April and 19 July 1978, after which smearing ceased for reasons unrelated to the experiment.

Where possible, females in each group were matched with litter-mates, or with females of approximately the same age.

RESULTS

BREEDING SEASON

Fig. 1 shows the monthly distribution of matings (directly observed or inferred from the subsequent birth of a litter — assuming a gestation period of

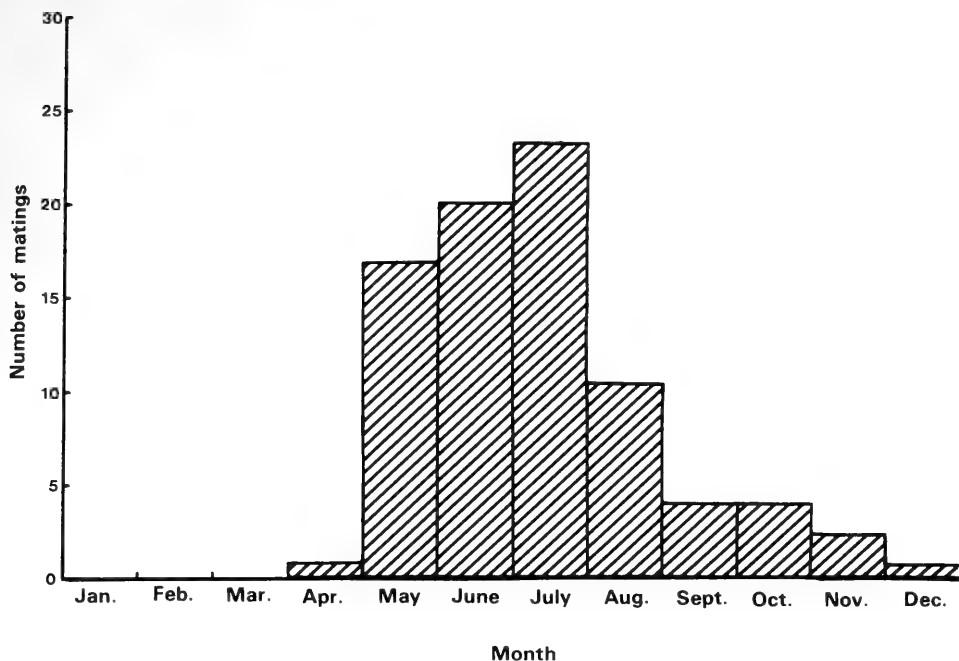


FIG. 1. The monthly distribution of matings in the colony of *D. byrnei* from May 1971 to December 1978.

35 days) in the laboratory colony from May 1971 to December 1978. The earliest mating in any year occurred on April 30th and the latest on December 22nd. Of a total of 103 matings, 75 (73%) occurred in May, June and July. As at least 25 pairs were caged together in every month of the year it is clear that the species has a strongly seasonal breeding pattern in captivity.

OESTROUS PERIODS

(1) *Paired females*

These 10 females showed one to four peaks of cornification in their cloacal smears, with peaks recurring at intervals of 49 to 86 days. The first peak detected from any female was on 26 April and the last on 8 December. Three females mated (as shown by sperm in their smears) at their first oestrus of the year, two at the second and one at the third. Sperm were seen in the cloacal smears of five of these six females between two and six days before maximum observed cornification, but the results from the sixth female were anomalous in that sperm were seen 12 days after maximum cornification.

The remaining four females failed to mate although two showed one peak of cornification, one showed three, and one four. No pouch development was observed in the first two females, but the third showed pouch development following her second peak of the year, and the fourth after her first and second peaks, which were separated by 61 days.

Of the six females which mated, four gave birth to a litter. Three of the four litters were successfully reared. No litters were found as a result of the other two matings, although pouch development had occurred.

(2) *Females caged individually but with males in the same room*

One of the females in this group died shortly after smearing began, but the remaining nine showed one to four peaks of cornification, separated by intervals of 42 to 120 days. The earliest was on 26 April and the latest on 15 December. Of a total of 25 detected peaks, only seven were followed by pouch development. The intervals recorded from two females which showed pouch development following each of two successive peaks in cornification were 55 and 64 days.

(3) *Females caged individually with no males in the same room*

Each female in this group showed either one or two peaks of cornification during the period smears were taken. Peaks occurred at intervals of 37 to 49 days, with the earliest being recorded on 17 May. No pouch development was seen following any of the 16 peaks recorded from these females.

INTERVALS BETWEEN PAIRING AND MATING

The pattern of intervals between date of pairing and mating reflected the seasonal breeding of the species. Table 1 shows the months in which pairs of animals were first caged together, and the range and mean intervals which elapsed before mating occurred. Only successful pairings (those which were known to have resulted in mating) were considered. Pairs were maintained for highly variable periods of time, and no rigid time-limit for mating to occur was used.

The mean interval between date of pairing and mating showed a monthly decrease from March to August, but abruptly increased in September and December, reflecting the fact that some of the pairs established in these months did not mate until the following year. The small mean intervals before mating for pairs established in October and November were a result of the fact that the females paired at this time were those which had lost or reared a litter earlier in the year, and many of these returned to oestrus shortly after lactation ceased.

On ten occasions pairs mated on the first day they were caged together. Nine litters were born as a result of these first-day matings, showing that ovulation had occurred.

BIOLOGY OF CAPTIVE *DASYUROIDES BYRNEI*

TABLE 1

Range and mean intervals which elapsed between pairing and mating for *D. byrnei* pairs established in different months of the year.

Month of pairing	No. of pairs	Range of intervals between pairing and mating (days)	Mean interval between pairing and mating (days)
Jan.	—	—	—
Feb.	—	—	—
Mar.	2	82 - 117	100.0
Apr.	25	5 - 194	66.9
May	30	0 - 175	37.8
June	10	1 - 78	31.3
July	10	0 - 88	19.2
Aug.	9	0 - 43	18.5
Sept.	7	6 - 286	121.0
Oct.	3	0 - 14	6.0
Nov.	5	4 - 21	12.8
Dec.	2	164 - 195	179.5
TOTALS	103	0 - 286	47.1

EFFECTS OF LACTATION ON OESTROUS CYCLING

Males were allowed to remain with females after the birth of their young on only two occasions and there was no evidence of sexual activity by these females while still suckling young. One female whose mate was allowed to remain with her while she reared her litter, mated again when the young were 138 days old. A second female which was re-caged with a male after her young were weaned at 113 days old, mated 13 days after removal of her young; and a third which was re-caged with a male immediately after her young were weaned at 104 days old, gave birth to a second litter 64 days later. Thus the intervals recorded between successive matings when the litter resulting from the first mating of the year was reared to weaning age ranged from 161 to 173 days.

Eight females lost their first litters of the year before weaning age and mated again during the same breeding season. The ages at which the litters were lost and the corresponding intervals which elapsed until mating were as follows:

Female No. 1;	litter lost at 24 days old,	mated 36 days later
2	37	7
3	49	0
4	51	9
5	56	5
6	56	5
7	67	7
8	67	1

LITTER SIZES, SEX RATIOS AND SURVIVAL OF YOUNG

Litter sizes in the I.M.V.S. colony have ranged between one and six. (No female with more than six teats has been found in the colony.) Of 79 captive-bred litters whose size was determined shortly after birth, the average litter size was 4.8. The frequency distribution of litter sizes was markedly skewed towards larger litter sizes, as the modal litter size was six. [Three births have been observed, and in one case seven young were born (D. Clyne, pers. comm.).]

In 38 litters which survived intact to weaning age, the sex ratio was 80 males to 98 females, which is not significantly different from one to one.

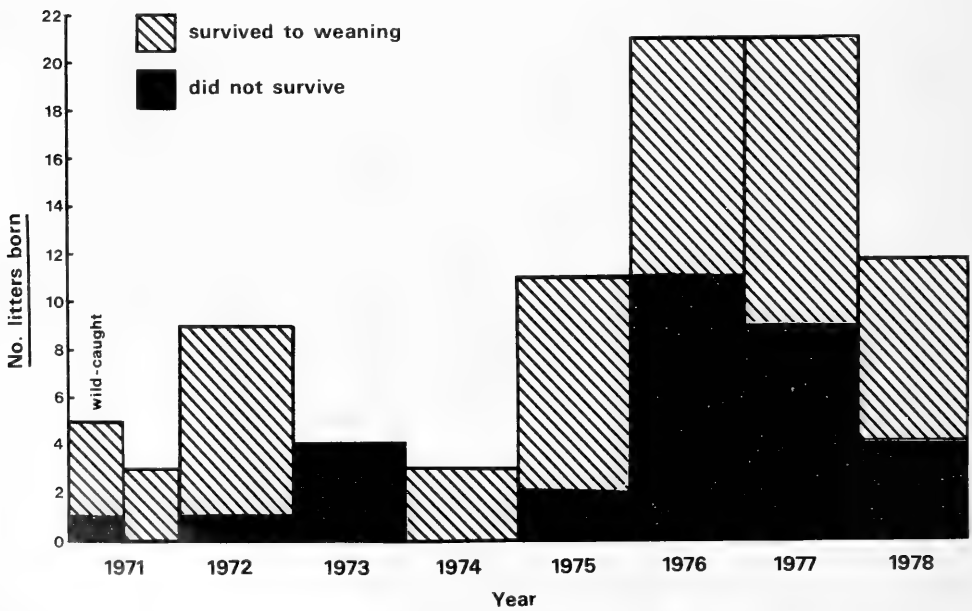


FIG. 2. Number of litters born per year from 1971 to 1978, and the proportion in which one or more young survived to weaning age.

Overall, of a total of 84 captive-bred litters, in only 51 (61%) did one or more young survive to weaning. Survival of litters varied markedly from year to year, and no young were weaned in 1973 (Fig. 2).

Thirteen of 32 litters lost (41%), were lost between 50 and 60 days of age (an accurate age when lost was not available for three litters). Six litters were lost at 60 to 70 days old, while the remaining losses were fairly evenly spread throughout lactation. Fifty to 60 days corresponds to the time at which the young are first detached from their mother's teats, and appears to be a critical stage in maternal behaviour.

Young were sometimes found scattered around their cage or partially cannibalised when they reached 50 to 60 days old. In the majority of cases where litters were lost, however, no traces of the young could be found and complete cannibalism by their mother was the only possible explanation of their disappearance. On those occasions when 50 to 60 day old young were found scattered around their cage they almost invariably appeared well-nourished and of normal size for their age, but were usually suffering from exposure. Such young were regularly replaced in their mother's nest (if she had built one), but they usually disappeared within a few days. Hyperactive females and females which failed to build nests frequently cannibalised their young.

SEXUAL MATURITY AND DURATION OF REPRODUCTIVE LIFE

The youngest female recorded as mating was aged 238 days (eight months), and the youngest male 216 days (seven months). There was no evidence that any young attained sexual maturity until the year following that of their birth.

The oldest female to have mated (and subsequently reared a litter) was aged 1,521 days (49 months), and the oldest male to have mated (and fathered a litter) was aged 1,471 days (48 months).

Although a number of animals survived to 50 or 60 months of age none bred after the fourth breeding season following birth, and very few bred after the third. For the majority of animals, therefore, reproductive life extended from about 10 to 40 months of age.

LONGEVITY

The maximum life-span of individual *D. byrnei* in the I.M.V.S. colony was 66 months for a female, and 65 months for a male. Both these animals were wild-caught, the female as pouch-young and the male as an independent juvenile.

NUMBER OF LITTERS BORN PER FEMALE

Forty-nine females gave birth to the 84 litters born in captivity. Twenty-four females gave birth to one litter, 16 to two, 8 to three, and one female gave birth

to four litters. Of those females which gave birth to more than one litter, eight produced two litters in one breeding season, but only one reared both litters. No female gave birth to more than two litters in any one breeding season.

The maximum number of young known to have been born to any one female over her lifetime was 19, and the maximum number reared to weaning age by one female was 15.

PAIRING SUCCESS RATES

Of a total of 250 recorded pairings, 103 (41%) were successful in that they resulted in mating being observed or a litter being born. The best pairing records for females were those of two laboratory-bred females which mated in each of four successive pairings. Several females mated in three out of four pairings, but others failed to mate even when they were paired successively with as many as seven different males. The best pairing performance by a male was that of an animal obtained from the wild as pouch-young; this male mated in six out of 11 pairings. Several males mated in five out of seven pairings.

During the period of study 80 females and 70 males were paired at least once. Of these, 56 (70%) of the females and 45 (65%) of the males mated at least once. Forty females that mated in their first pairing were subsequently re-paired. Twenty (50%) of these also mated in their second pairing.

Of those animals which failed to mate in their first pairings, 33 females and 32 males were subsequently re-paired on one or more occasions. Only 9 (27%) of these females and 7 (22%) of the males eventually mated. Thus it is evident that second and later pairings of animals which had not mated in their first pairing were relatively unsuccessful.

REARING OF YOUNG BY WILD-CAUGHT AND CAPTIVE-BRED FEMALES

Thirteen litters were born in captivity to wild-caught females, and in 11 of these (85%) at least one young survived to weaning. Seventy-one litters were born to captive-bred females, but in only 40 (56%) did one or more young survive to weaning.

CAUSES OF DEATH OR INJURY AFTER WEANING

In the first few years after establishment of the colony it was found that caging either mixed-sex or same-sex litter-mates in groups after they attained sexual maturity led to many deaths. Members of such groups were often found partially cannibalised. Therefore, such litter-mate groups were separated before their members became sexually mature. Under the present husbandry régime all adults are caged individually unless they have been paired with a member of the opposite sex for breeding purposes. With this régime few animals died as a

result of aggression from cage-mates. Most injuries due to fighting occurred in the first week after new pairs were established.

In most cases newly-paired animals were watched for the first 10 to 15 minutes they were caged together, and were separated immediately if they proved incompatible. This was indicated if one animal persistently chased the other, or locked fighting occurred. If it was necessary to separate the animals on the first day they were paired, no record of the attempted pairing was made.

Of 147 unsuccessful pairings (those which lasted for more than one day, but did not result in mating being observed or young born), a specific reason for separation of the pair was recorded in 52 cases. (The majority of separations were to allow routine re-pairing of animals which had failed to mate.) In 16 cases, termination of the pairing was due to the death of one member — in 14 of these the female died, and in 2 the male. The high incidence of cannibalism seldom allowed definite causes of death to be established for animals which were paired. In 32 cases, pairs were separated due to aggression by the female towards the male, resulting in him losing weight, having his tail bitten or back scratched. One female castrated two males with which she was paired. Only four cases of pairs being separated due to aggression by the male towards the female were recorded.

In 12 of 35 animals submitted for post-mortem examinations, toxoplasma-like pseudocysts were detected histologically in the brain or other organs, and/or the presence of toxoplasma infection was demonstrated in mouse-transmission tests. In six of these cases, infection by *Toxoplasma gondii* was associated with severe congestion of the lungs and areas of necrosis or exudative pneumonia. In two other cases the animals showed evidence of haemorrhagic enteritis associated with the toxoplasma infection.

External symptoms observed in animals found at post-mortem to have toxoplasma infections included balding of the tail and hind-quarters, cataract formation in one or both eyes, and progressive weakness in the hind-legs. Some or all of these symptoms were observed in a further eight animals which died but were not submitted for post-mortem examination. The youngest animals in which these symptoms were seen were aged two years, but the majority were four years old or more. Attwood *et al.* (1975) have reported similar findings from the LaTrobe University colony of *D. byrnei*, and in accordance with their suggestion that the animals contracted the disease from eating infected raw meat, the diet of animals in the I.M.V.S. colony was modified in 1975 to eliminate this source of infection (by cooking the minced meat and feeding the animals *Toxoplasma*-free mice). No *Toxoplasma* infections have been detected to date among animals fed this diet since weaning although transmission via cannibalism is possible.

In January 1978, 13 animals died over a period of five days. All but one were young born in the previous year. Post-mortem examinations suggested death

was due to a toxin which caused haemorrhage into the gastro-intestinal tract, severe nephritis, and fatty change, haemorrhage and centrilobular necrosis of the liver. The cause of the deaths was thought to be food-poisoning possibly due to a toxin produced by a strain of *Clostridium welchi*. All the animals which died during this period were found to have pronounced mineralisation of the kidneys, which probably rendered them especially susceptible to the effects of the toxin. Other animals which had been fed the same food showed no ill-effects. The cause of the mineralisation was not established.

Other postmortem findings included one animal which died as a result of bacterial mastitis and septicaemia following the weaning of her young, and one animal which died as a result of blood loss after the rupture of a splenic tumor. One further animal contracted "lumpy-jaw", similar to that observed in many macropods, and after death was found to have a severely deformed lower jaw.

DISCUSSION

The general pattern of reproduction observed among captive *D. byrnei* was similar to that of other polyoestrous dasyurids such as *Sminthopsis macroura* (Godfrey, 1969a as *S. larapinta*), *S. crassicaudata* (Ewer, 1968; Smith *et al.*, 1978) and *Planigale maculata* (Aslin, 1975 as *Antechinus maculatus*). Gestation and duration of lactation were longer in the larger *D. byrnei*, but litters smaller and thus the maximum reproductive rate of *D. byrnei* is considerably lower than that of these three species. Evidence from the present study suggests that the maximum number of young which a female *D. byrnei* could rear in one breeding season is 12. If females lost the first litter of the season before weaning age they sometimes returned to oestrus immediately, but there was no evidence of an immediate post-weaning oestrus as occurs in *S. crassicaudata* (Godfrey, 1969a).

The observed rate of breeding in the captive colony was far below the potential maximum. The seasonal breeding pattern observed in the wild was maintained in the laboratory over the eight year period, but few matings were observed from August to December, although many pairs which had failed to mate earlier in each year were still caged together during this period, or were re-paired. Few females mated twice in any one breeding season, and only one female succeeded in rearing two litters to weaning age in one breeding season. Thus it seems that the second peak of sexual activity thought to occur in wild populations after the weaning of the first litter of the year was largely suppressed in the laboratory environment.

The cloacal smear data presented here could not be interpreted as providing good evidence of an endogenous oestrous cycle in *D. byrnei*.

At least three explanations are possible:

- (1) the technique used was unreliable in detecting oestrus
- (2) captive conditions resulted in the animals experiencing many irregular cycles

- (3) *D. byrnei* does not have an endogenous oestrous cycle but is an induced ovulator.

Evidence from paired females showed that at least some observed peaks in cornification did correspond with behavioural oestrus, and were followed by pouch development and birth at the expected time. If the technique is accepted as valid, an explanation must then be found for the irregular recurrence of oestrus and lack of pouch development observed in many females.

Godfrey (1975) has reported that the absence of mammary development following oestrus in mouse opossums (*Marmosa robinsoni*), a marsupial which lacks a pouch, is an indication that the oestrous cycle was anovular. By analogy, failure of pouch development in *D. byrnei* females after oestrus may also indicate that ovulation has not occurred. If this is so, both the irregular cycles observed and absence of pouch development may result from failure of females to ovulate under captive conditions. The fact that pouch development failed to occur in any of the females completely isolated from males suggests that stimuli provided by the presence of males may be a necessary prerequisite for ovulation, in addition to appropriate day-length cues.

Ten first-day matings were recorded between pairs of *D. byrnei* in the colony, and nine of these matings were followed by the birth of a litter. This suggests that simply pairing a female with a male during the breeding season was, on some occasions, sufficient to induce immediate oestrus, and that ovulation ensued. This appears similar to the "Whitten effect" described for laboratory *Mus musculus* (Whitten, 1956). Alternatively, these observations could also be interpreted as being consistent with the occurrence of induced ovulation. Further data are necessary to decide between these alternatives.

The finding that first pairings for both sexes of *D. byrnei* more often resulted in mating than subsequent ones is similar to that reported by Smith *et al.* (1978) for their colony of *Sminthopsis crassicaudata*, in which 44 of 77 females which produced at least one litter, gave birth to a litter fathered by the first male with which they were paired after reaching maturity. In addition, 15 of these matings occurred within four weeks of the pair being established. Smith *et al.* (1978) also found that significantly more females produced a second litter when re-paired with the father of the first than did those which were re-paired with a different male.

Although data were not adequate to examine this "compatibility effect" in the *D. byrnei* colony, the "recency effect" appeared to be even more pronounced. Of the ten pairs of *D. byrnei* that mated on the same day they were first caged together, six involved a female which was paired for the first time. Thus there seems little doubt that being newly-paired, and particularly being newly-paired for the first time, provided the most favourable situation for mating to occur under laboratory conditions.

Apart from the low incidence of mating from August to December, the other major reason for the sub-optimal breeding of the *D. byrnei* colony was that a large number of litters were cannibalised by their mothers. Cannibalism is a common problem among laboratory colonies of small mammals, and the observations made on cannibalism in *Peromyscus* colonies (King, 1963) were similar to those made in the present study, except that cannibalism in *D. byrnei* commonly did not occur until the young were about eight weeks old, while in *Peromyscus*, young were usually eaten at or shortly after birth. Causes suggested for cannibalism in various species have included nutritional deficiencies, absence of suitable nest-sites (King, 1963), genetic factors (Ross *et al.*, 1963) and "social stress" (Martin, 1975).

In the *D. byrnei* colony it was found that wild-caught females lost very few litters, and that failure to rear young (usually due to cannibalism), only became a major problem when most of the colony consisted of captive-bred animals. Similar problems of poor litter survival have also been experienced with captive colonies of the small dasyurids *Planigale maculata* (unpublished data) and *Sminthopsis macroura* (Godfrey, 1969a), although in the latter case, loss of litters was not definitely attributed to abnormal maternal behaviour. Interestingly, in the *P. maculata* colony, decline in both number of litters born and in the percentage which survived to weaning, was arrested by the introduction of a small number of wild-caught animals (unpublished data).

The fact that newly-introduced wild-caught animals breed and successfully rear their young under the same captive conditions in which laboratory-bred animals fail to do so, strongly suggests that these conditions are not in themselves responsible for the decline in breeding. Presumably one must look to changes in the animals themselves and in their reactions to the laboratory environment: either genetic changes over successive generations in captivity, abnormalities in the development of young due to inadequacies in the laboratory environment, or to some interaction between these factors.

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Some Aspects of the Reproductive Biology of *Parapallene avida* Stock (Pycnogonida: Callipallenidae) from Northern New South Wales

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ABSTRACT

The life-history, reproductive biology and age structure of *Parapallene avida* were investigated over a period of 8 months in 1976, with additional observations made in 1978.

Mating was observed on two occasions and involved courtship, copulation, and a process whereby the male cements the eggs to his ovigerous legs. Males are capable of mating more than once per breeding season, whereas females apparently mate only once per season. Breeding was observed mainly during summer and autumn, although the complete reproductive cycle was not determined.

Egg cleavage was total, but unequal sized blastomeres were formed. Larval development was anamorphic, and the newly hatched protonymphon possessed little metamerism, which nevertheless gradually increased as development progressed. The first two instar stages developed while on the male's ovigers, but older larvae assumed an association with various hydroid species. The period from fertilisation of the ova to hatching of the first instar larva was approximately 5 weeks. The second moult followed one week later.

INTRODUCTION

The reproductive biology of Australian pycnogonids, or "seaspiders", has received little attention. However, studies on pycnogonids of Great Britain, India, Antarctica, United States and Japan have shown that many have a peculiar system of larval brooding, whereby the male sticks the eggs to his ovigerous legs in clusters, immediately following copulation with the female (Morgan, 1891; Cole, 1910; Gnanamuthu, 1950; King and Jarvis, 1970; Sekigushi *et al.*, 1971; Jarvis and King, 1972 and 1975). These clusters may contain eggs produced from more than one mating.

The nauplius-like larva, called a protonymphon undergoes a series of moults, eventually taking on the appearance of the adult. In some species the larva leaves the male and becomes associated with organisms such as hydroids, bryozoans and actinarians, on which it feeds. In other species the larva remains with the male until metamorphosis is complete (King, 1973).

This paper presents observations on the life-history, population structure and reproductive biology of *Parapallene avida* Stock, 1973 from Arrawarra Headland, New South Wales (30° 05'S, 153° 15'E). Although this species has been reported previously only from Western Port Bay and Gabo Island, Victoria (Stock, 1973a and b), further sampling may show that it is distributed widely in *Sargassum* seaweed of the sublittoral zones along the south-eastern coast of Australia.

MATERIALS AND METHODS

The study area encompassed 9075 m² of rock platform, with a north to north-eastern aspect, extending into the sublittoral zone to a depth of 2.5 m below the mean spring tide level.

Specimens of *P. avida* were collected by random sampling of seaweed. The area was divided into 4 equal sized transects, each of which was subdivided into smaller areas using approximate depth contours. Individual subdivisions were then selected at random, and a 600 x 600 mm metal quadrat was cast into the subdivision to locate samples. All macrophytes lying within this quadrat were taken.

Sixty-one samples of macrophyte, comprising 9 species, were examined each month from February to September, 1976. Several additional samples were collected in March and April, 1978 for studies on mating and larval growth of pycnogonids.

To extract pycnogonids from the macrophytes, the method of Vollenweider (1969) was modified as follows. Each plant was placed in a solution of 5% formalin in freshwater for 30 minutes, agitated rapidly for 5 minutes, washed with a jet of freshwater, and then poured through a series of sieves (0.5 and 1.0 mm mesh sizes). Animals were then further fixed in formol-alcohol (Humason, 1967), and stored in 70% ethanol.

Specimens of *P. avida* were assigned to a reproductive and developmental class according to characters shown in Appendix I.

The ovary and/or eggs, lying within the female's femurs, were examined unstained, and oocytes were classed on the basis of size and colour (Schmidt, 1971) as either previtellogenic (with thin membranes, lightly opaque and less than 100 µm in diameter) or vitellogenic (with thick membranes, opaque-white to yellow and between 100 and 250 µm in diameter).

Some additional live specimens were collected and maintained in aquaria for studies on mating and larval development. Adults were kept in aerated aquaria (measuring 900 x 400 x 400 mm) containing *Sargassum* with a dense coverage of various hydroid species. These aquaria were exposed to natural light but temperature was maintained between 23 and 24°C.

Several adult males and females were placed on the *Sargassum* and were then left undisturbed for 2 days. Their activities at 6-hourly intervals were then recorded (for various durations) until mating behaviour was observed.

REPRODUCTIVE BIOLOGY OF *PARAPALLENE AVIDA*

Floodlights were initially used to locate animals on the seaweed. Once located, these lights were turned off, and observations were continued in daylight, or by dim lamps at night. Unlike the planktonic species (Cole, 1910), strong light seemed to have little effect on the activity of this species.

Eggs from one male which had recently mated, were brushed from the ovigers into a smaller aerated aquarium (measuring 350 x 200 x 200 mm), also containing fragments of *Sargassum* covered with hydroids. This aquarium was subjected to the same temperature range and light conditions as described above.

To minimise the possibility of bacterial infection of the embryo, 200,000 i.u. (~ 130 mg) per litre of seawater of phenoxymethylpenicillin (Falcopen VK, "Faulding") was added (Cameron, 1965). Subsequent larval development was observed over a period of approximately six weeks. Eggs and larvae at various stages of development were fixed in formol-alcohol, cleared and examined in lactophenol creosote.

Drawings of these were made with the aid of a camera lucida, and they were measured using a calibrated ocular micrometer. The trunk length of all pycnogonids was measured from the anterior end of the cephalon to the base of the anal tubercle, following the method of Jarvis and King (1972).

RESULTS AND DISCUSSION

ABUNDANCE

From a total of 488 seaweed samples, 62 adult *P. avida* males, 61 females, 39 immature animals, 57 'free-living' protonymphon larvae and approximately 350 eggs and larvae attached to males' ovigers were obtained.

Parapallene avida represented only 12% of the total number of pycnogonids sampled. Other species collected (and their percentage relative abundances) included *Nymphopsis acinacispinatus* Williams (10%), *Pycnothea flynni* Williams (1%), *Pycnogonum rickettsi* Zeigler (0.4%), *Pycnogonum* species (0.5%), *Tanystylum hooperi* Clark (12%), *Tanystylum* species A (13%), *Tanystylum* species B (0.1%), *Anoplodactylus* species A (42%) and *Anoplodactylus* species B (9%).

Individuals of *P. avida* were found on the seaweeds *Sargassum neurophorum*, *S. lophocarpum*, *S. cristatum* and *Neurocarpus asrotichoides*, mainly in association with the hydroids *Campanularia* sp., *Clytia* sp. and *Kirchenpacceria* sp.

SEASONAL VARIATION IN AGE STRUCTURE

The age structure of the *P. avida* population varied seasonally, with the adult population at a peak in February (summer) ($\chi^2 = 54.80$, $P < 0.001$) and the protonymphon larval population at a peak in August and September (winter-spring) ($\chi^2 = 23.96$, $P < 0.001$) (Figure 1A).

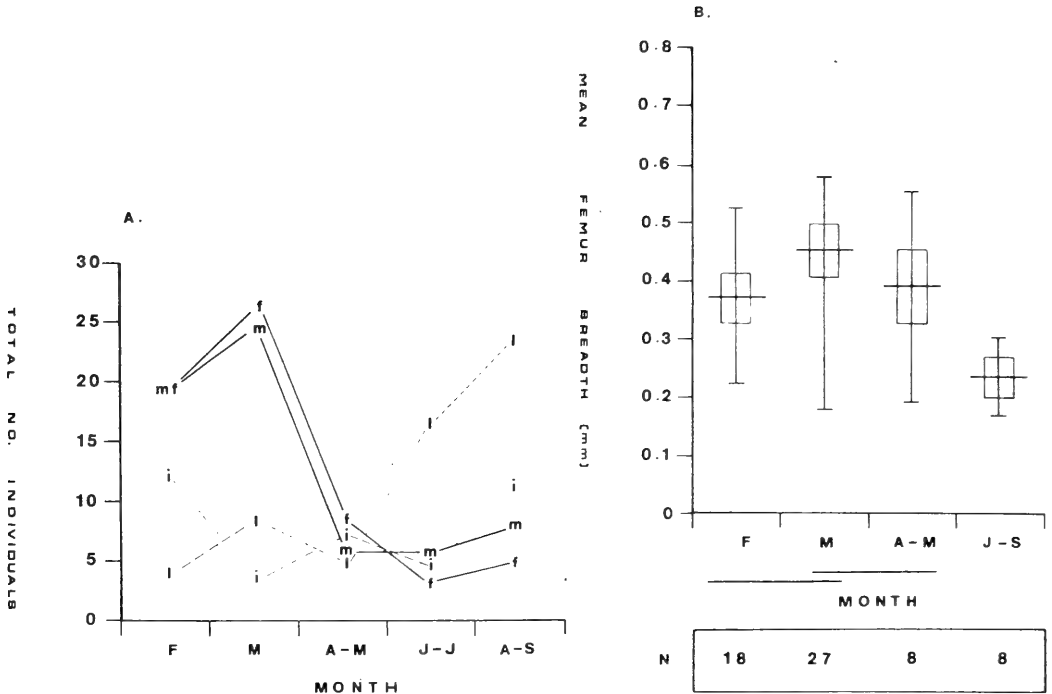


FIG. 1. A. Distribution of life-history stages of *P. avida* during 1976.

m — Adult males; f — Adult females; i — Immature animals; l — 'Free-living' protonymphon larvae.

B. Seasonal comparisons in adult female femur breadths of *P. avida*, indicating the mean (horizontal lines) \pm 2 standard errors (vertical rectangles) and range (vertical lines) of measurement (in millimetres). The results of a 1-Factor analysis of variance are given below, and results of Student-Newman-Keuls tests are shown by lines connecting months not showing significant differences.

SOURCE	DF	MS	F	SIGNIFICANCE
MONTHS	3	0.106	11.281	P < 0.001
ERROR	57	0.0094		

Monthly differences in the mean number of 'free living' protonymphon larvae may be attributed to an increase in the number of larvae leaving parental males during the latter half of the year, whereas during the earlier months, these larvae are probably attached to the male's ovigers. Whether adults die in winter or migrate is not known. Their relatively low numbers in winter may be related to the seasonal growth of hydroids (a probable food source), which are reportedly less common in winter than in spring and summer (King, 1973) at least in northern temperate regions.

REPRODUCTIVE BIOLOGY OF *PARAPALLENE AVIDA*

The number of immature animals was at a peak in February, August and September ($\chi^2 = 11.36$, $P < 0.025$) which may indicate that metamorphosis from the protonymphon stage occurs during spring and summer.

Upon reaching maturity, the female's femurs become distended with the developing ovary. Femur distension (breadth) was greatest from February to April (Figure 1B), which suggests that this is the breeding period. However, breeding may also occur during the early summer months, which were not sampled.

The simultaneous presence of eggs and recently hatched larvae on the ovigers of males indicates that they are capable of mating more than once during a breeding season (Table 1). The composition of these egg and larval clusters shows that during the months February and March, all clusters held by males contain only eggs, whereas during later months, only clusters of protonymphon larvae are present.

The data of age-class distribution, female femur distension and the composition of clusters held by males all indicate a breeding season in the summer — early autumn period. This has also been proposed as the breeding season of *Pycnogonum littorale* in the northern hemisphere (Jarvis and King, 1972). However, the absence of data from October to January in the present study makes it impossible to determine the extent of breeding throughout the year.

Neither age at maturity nor longevity are known for *P. avida*. Figure 1B and Table I suggest that most adults die during winter judging from their abundance in the samples, but it is possible that emigration from the rock platform is the cause of the low numbers found at that time. Jarvis and King (1972) found that age at maturity is approximately 12 months for *P. littorale* from the U.K. and suggested that longevity of this species is several years.

TABLE 1. Monthly comparisons of the mean number of egg and larval clusters on the ovigers of adult *P. avida* males.

Number of clusters	MONTHS			
	February	March	April-May	June-September
Males with 4 clusters of larvae	0	0	0	1
Males with 2 clusters of larvae	0	0	0	3
Males with 2 clusters of larvae and 2 of eggs	0	0	2	0
Males with 2 clusters of eggs	3	4	0	0
Males without egg or larval clusters	15	20	4	10
Total No. adult males sampled	18	24	6	14

MATING

Mating was observed on two occasions, and both matings showed similar patterns of behaviour. Each mating lasted for approximately four and a half hours (270 and 253 minutes respectively). Both courtship and copulation were observed. Courtship lasted for approximately half an hour (32 and 24 minutes), and commenced with the male closely following the female at a distance of less than 30 mm. On several occasions, the male approached the female with his anterior pair of legs raised, and with these, touched the female's posterior pair of legs. When touched, the female moved to a different location.

After several such approaches, the male climbed upon the female's dorsal surface, orientated head to head. The male clasped the female's first pair of legs and trunk with his first and second pair of legs respectively. They remained in this copulatory position for approximately three and a half hours (213 and 198 minutes), the male moving his second pair of legs occasionally during this time.

This copulatory position of *P. avida* is similar to that described for *P. littorale* (Jarvis and King, 1972). Unlike *P. littorale*, which is known to maintain the copulatory position for up to 5 weeks *P. avida* mated for much shorter durations. Other records of mating behaviour show that *Anoplodactylus lentus*, *Phoxichilidium femoratum* and *Endeis laevis* copulate with opposing ventral surfaces in contact, and orientated head to tail (Hoek, 1881; Cole, 1901; Loman, 1907; Prell, 1910; Jarvis and King, 1972; King, 1973).

During copulation, it was observed that the male of *P. avida* often brought his legs into contact with the female's legs, the male's second pair being most active. It is possible that fertilisation occurred during this behaviour, as the genital pores are situated on the femur-coxa junction of all legs, the male's pores located ventrally and the female's pores located dorsally. King (1973) recorded that males and females of *P. littorale* have genital pores situated on the ventral and dorsal aspects of legs respectively, and during mating these orifices actually touch. Whether or not sperm transfer occurred at that time was not reported.

Using his ovigers, the male collected between 5 and 8 eggs from each of the female's femurs, giving a total of 52 and 60 eggs respectively from each mating. On completion of egg collection, the males had 2 clusters of eggs, one on each oviger, and each cluster contained approximately 30 eggs. Examination of other egg-bearing males showed that this number of egg-clusters (2) (Table 1), and number of eggs in each cluster (between 21 and 35) was relatively constant for this species.

The male held these eggs by curling his ovigers towards the ventral surface of his body, so that on completion of egg collection, almost all the ten oviger segments were covered with eggs. Retaining the eggs on the ovigers was probably facilitated by the numerous oviger spines possessed by males, (Figure 2, A, B and C), and by the egg's sticky hyaline coat.

REPRODUCTIVE BIOLOGY OF *PARAPALLENE AVIDA*

After copulation, the female moved away from the male, which remained in a similar stance as when copulating. This position was maintained for about half an hour (25 and 31 minutes), during which time the male moved his egg-laden ovigers, frequently bringing them into contact with one or more of his ambu-

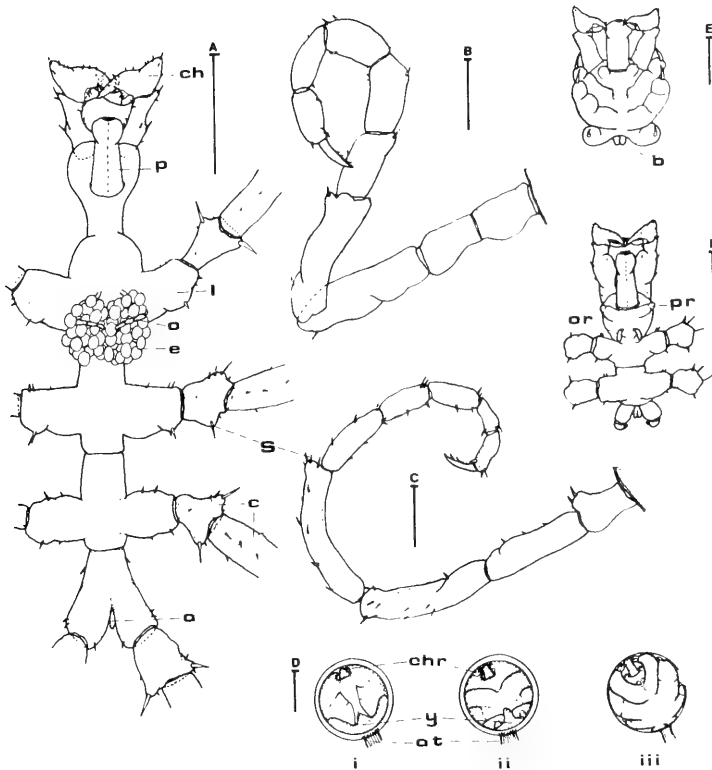


FIG. 2. Morphology and larval development of *P. avida*.

(A) Egg-laden male adult (1000 μm). (B) Female's ovigerous leg (100 μm). (C) Male's ovigerous leg (100 μm). (D) Post-gastrula and first instar larval stages (200 μm). (E) Second instar larva after moulting — still attached to male's oviger (250 μm). (F) An immature specimen with 2 pairs of legs and the rudiments of the third pair (500 μm).

Key to lettering: a — abdomen; at — stalk for attachment; b — buds of developing legs; c — coxae; ch — chelifore; chr — chelifore rudiment; e — egg masses; l — lateral process; o — oviger; or — oviger rudiment; p — proboscis; pr — palp rudiment; s — setae; y — yolk remnants.

latory legs. This behaviour probably serves for cementing the eggs together, because in many species, the cement glands are situated in the coxae or femurs of some or all the male's legs (King, 1973). Because the hyaline coat of the egg hardens rapidly on contact with seawater, it is unlikely that fertilisation of the eggs occurs during this later behaviour.

Although it is not known whether the female released all her mature (vitellogenic) eggs during copulation, examination of other females in "spawning" condition (Appendix I) did not reveal more than 8 or 9 vitellogenic oocytes present in any single femur, thus suggesting that all eggs are released during copulation.

By comparison, females of *Endeis spinosa* and *Nymphon gracile* release mature eggs from only a few of their femurs during a single mating. King and Jarvis (1970) and King (1973) suggested that this behaviour enables the females of these species to mate more than once during a breeding season, possibly with more than one male, thus ensuring the dispersal of larvae from each female. In contrast, females of *P. littorale* are similar to *P. avida* in that they release all their mature eggs during one mating. These eggs are subsequently gathered into a single mass by the male (Jarvis and King, 1972). For this reason, Jarvis and King suggested that females of *P. littorale* are able to mate only once during a breeding season, but whether males of that species mate more than once is unknown.

P. avida showed a third type of reproductive strategy whereby the females may release all their mature eggs during one mating, thus being able to mate only once in a breeding period, but males are capable of mating with more than one female during this period.

LARVAL DEVELOPMENT

Experiments on *in vitro* brooding of embryos were only partially successful, since only the second-moult larval stage was ever reached.

Initial division of the ovum was total, and subsequent divisions produced blastomeres of unequal size. Cleavage continued until the blastula consisted of a narrow distal region of small micromeres and a proximal region of larger macromeres (closest to the centre).

As a result of gastrulation, an endoderm or yolk-rich syncytium is formed. The yolk is visible in the embryo for a large part of its later development, but finally disappears during metameric segmentation of the early protonymphon (termed the "embryonic" or "sechsfüssige" larva) (Gnanamuthu, 1950; Sekigushi *et al.*, 1971), (Figure 2D, i, ii and iii).

Cleavage and gastrulation of the eggs of *P. avida* were similar to that described for *Propallene kempfi* and *P. longiceps* (Gnanamuthu, 1950; Sekigushi *et al.*, 1971), all of which have heavily yolked eggs which undergo total cleavage (King, 1973).

The *in vitro* period from fertilisation to gastrulation took from 16-18 days. A further 12-15 days elapsed before the embryo showed evidence of development of rudimentary appendages. The embryonic larva, with the chorion still intact, lasted 6-7 days, and the second moult occurred 7-10 days after hatching. This second instar showed little metamerism (Figure 2E), which is characteristic of organisms with an anamorphic larval development (Sanchez, 1959).

In vitro studies were successful in demonstrating first and second instar larvae. *In vivo* observations showed that these larvae were carried on the male's ovigers and they were not normally found independent of the adult male. It appears that the protonymphon of *P. avida* leaves the male and assumes a 'free-living' existence sometime between the second and third larval moults. Sekigushi *et al.*, (1971) termed this first 'free-living' protonymphon of *P. longiceps* the "swimming larva".

Dogiel (1913; reported in Jarvis and King, 1972) proposes 7 larval instar stages necessary to complete metamorphosis to the adult. The possible 5 remaining instar stages of *P. avida* would develop after the larva attaches itself to hydroids or other substrata. In the absence of experimental evidence, these stages could not be separated reliably and hence were considered together as 'free-living' protonymphon in this present study. In the experimental aquarium containing second instar larvae, several of these were found attached to zooids of hydroids (*Kirchenpacceria* sp.), using their already well-developed chelifores for adhesion. Whether this hydroid is a usual substratum for these larvae is not known, as further larval development was not observed *in vitro*.

From *in vivo* observations, the ensuing development of the larva involves a progressive increase in the number of legs, oviger and leg segments and pigmentation of the cuticle, eventually culminating in a post-instar, immature stage, which has a full complement (4 pairs) of fully-segmented legs (Jarvis and King, 1972). Subsequent growth occurs by further moulting (King, 1973), accompanied by an increase in the number of oviger segments (to 10), and an increase in pigmentation (dark red to brown in colour) of the body wall.

CONCLUSIONS

Further studies are required to determine the extent of the breeding period of *P. avida*, but present results suggest a summer-autumn breeding season.

Although there are similarities in the mating behaviour of *P. avida* and the British *P. littorale*, it seems that many interspecific differences exist. Present data suggest that females release all mature oocytes during one mating, and hence are thought to mate only once, whereas males are capable of mating more than once during a breeding period.

Larval development of *P. avida* is similar to those species with relatively large, heavily yolked eggs. At least two instar stages are achieved on the male's ovigers, and evidence suggests that subsequent larval moults occur while larvae are attached to hydroids.

ACKNOWLEDGEMENTS

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REPRODUCTIVE BIOLOGY OF *PARAPALLENE AVIDA*

APPENDIX I. Summary of a classification scheme used to assign individuals of *P. avida* to an appropriate reproductive and development class.

STAGE	CHARACTERISTICS
1. ADULTS	Pigmentation of cuticle complete (red-brown); 4 pairs of fully developed legs; 10 oviger segments; distinct sexual polymorphism.
Males	3.56-4.24 mm trunk length (T.L.); ovigers with numerous setae and 0.95-1.25 mm long; range of femur breadth from 0.18-0.32 mm.
Females	3.97-4.61 mm T.L.; ovigers with few setae and 0.80-0.90 mm long; femurs 0.15-0.69 mm wide containing developed ovaries.
2. IMMATURE STAGES	1.50-3.50 mm T.L.; pigmentation (light brown) of cuticle incomplete; 4 pairs of fully formed legs; ovigers 5-9 segments; sexual polymorphism sometimes distinct; gonads undeveloped.
3. 'FREE-LIVING' PROTONYMPHON	0.60-1.50 mm T.L.; cuticle pigmentation absent to light brown; ovigers 2-4 segments; legs and leg segments incompletely developed, i.e. ranging from 2 pairs of fully formed legs with buds of third pair present posteriorly, to 4 pairs of legs, the anterior 3 pairs of which are fully segmented.
4. 'ASSOCIATED' PROTONYMPHON	0.2-0.5 mm T.L.; includes all larvae residing on ovigerous legs of males: i.e. second instar larvae with 1-2 segmented legs and chelifores, and segmented ovigers and palp rudiments; first instar larvae with single segmented legs, chelifores, ovigers and palps and with chorion intact, and pre-gastrula and gastrula embryos with little or no metamerism.

Fish Kills in Relation to Physical and Chemical Changes in Magela Creek (East Alligator River System, Northern Territory) at the Beginning of the Tropical Wet Season

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ABSTRACT

Fish kills at the beginning of the wet season are frequently observed in the tropical coastlands of the Northern Territory. The sequence of flushes of the lagoons in the Magela Creek system for the 1978/1979 wet season and the associated fish kills are documented in this paper.

Low dissolved oxygen levels most likely caused a large fish kill observed at Leichhardt lagoon. These results indicate one of many possible mechanisms explaining natural fish kills in tropical freshwaters of Northern Australia. Determining the differences between man-induced and natural fish kills is very difficult owing to our scant knowledge of factors and mechanisms which effect fish survival in such waters.

INTRODUCTION

Magela Creek ($12^{\circ}16'$ to $12^{\circ}59'S$; $132^{\circ}52'$ to $133^{\circ}8'E$) is a seasonal tributary of the East Alligator River in the tropical 'top-end' of the Northern Territory (Figure 1). Flow in this creek system usually starts in December following rains commencing a month or so earlier at the beginning of the tropical wet season (Figure 2). Few limnological observations (Hart and McGregor 1978) have been made on the beginning of flow in this creek (on which two of Australia's largest uranium deposits, Ranger and Jabiluka, are located) and the subsequent flushing of the permanent water-bodies in the system.

Fish kills at the beginning of the wet season are frequently observed in the tropical coastlands of the Northern Territory. This paper documents the sequence of flushes for the 1978/1979 wet season and the associated fish kills. Water quality and other environmental data are presented in an attempt to explain the association between the beginning of creek flow and the observed fish kills.

STUDY AREA

A general description of the Magela Creek catchment is given by Hart and McGregor (1978) and Williams (1979). The locations of the Magela Creek

lagoons mentioned in the text are shown in Figure 1. Brief outlines of the known biology of the freshwater fish species inhabiting this area (including those involved in the fish kills) are given by Pollard (1974).

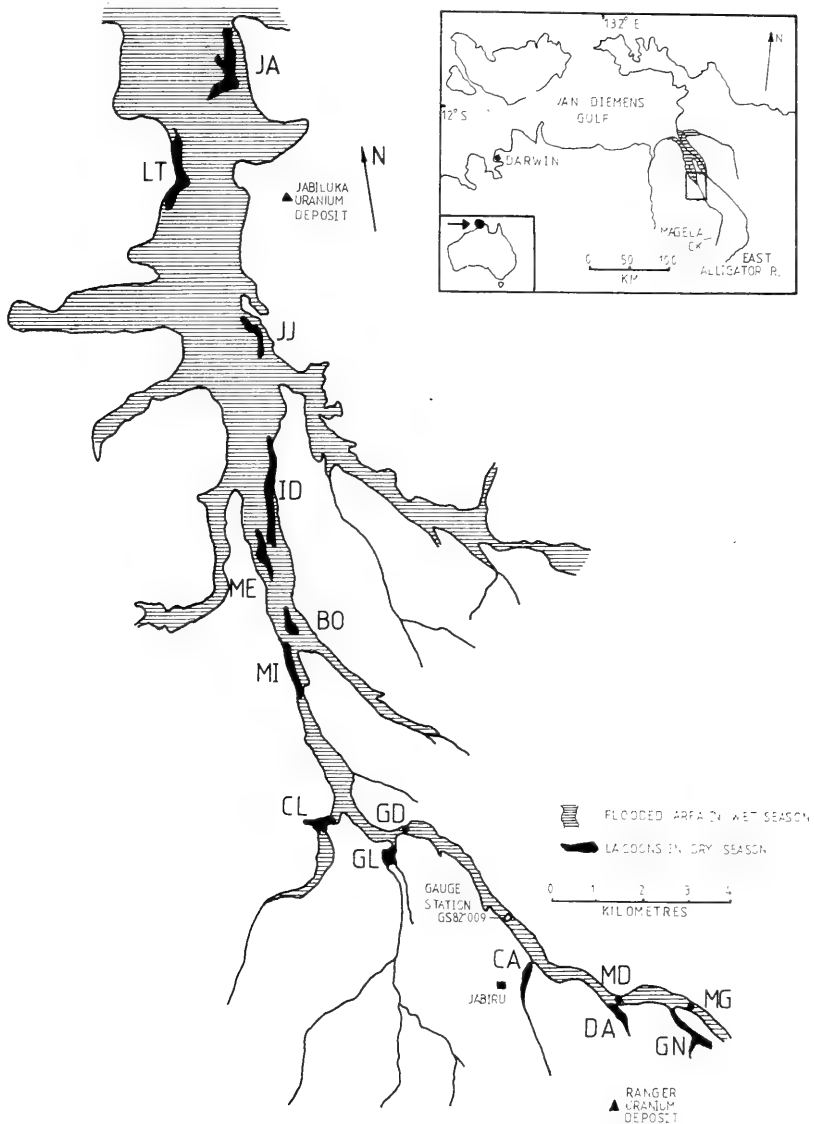


FIG. 1. Magela Creek catchment showing lagoon sites mentioned in text. Lagoon site codes: JA, Jabiluka; LT, Leichhardt; JJ, Ja Ja; ID, Island; ME, Mayamarleprard; BO, Buffalo; MI, Mudginberri; CL, Corndorl; GL, Gulungul; CA, Coonjimba; D.A., Djalkmarra; GN, Georgetown; GD, MD and MG, Magela Creekbed sites.

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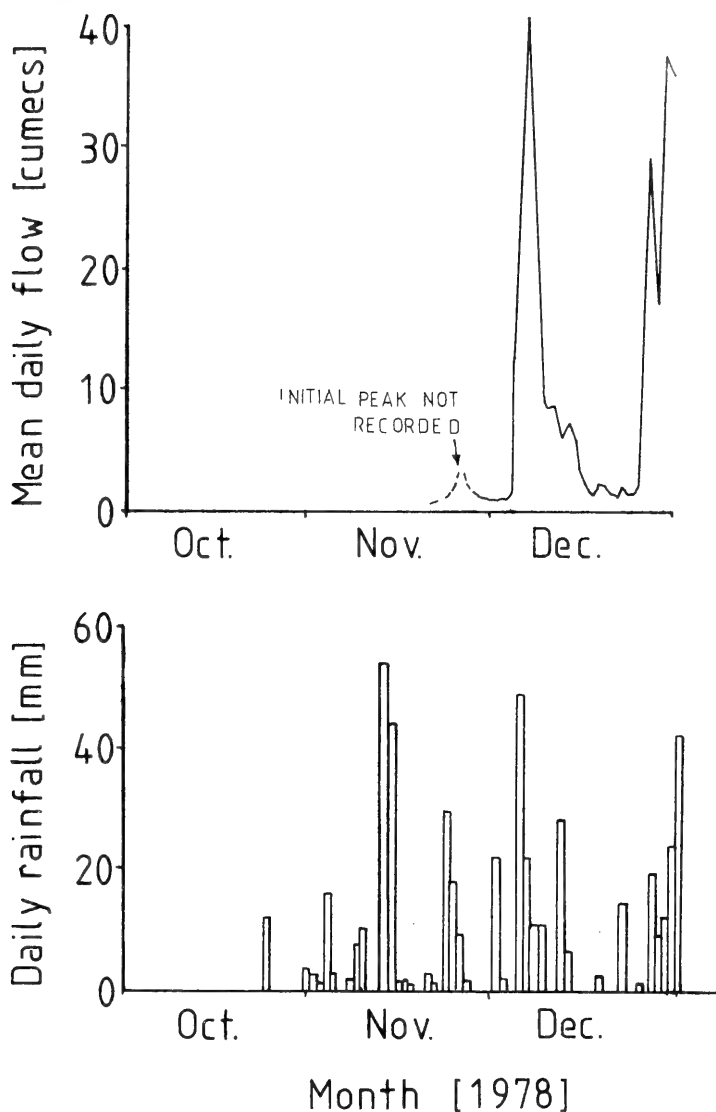


FIG. 2. Rainfall and Magela Creek flow (at GS821009) near Jabiru during the commencement of the 1978/79 wet season.

The five backflow lagoons studied (Georgetown, Djalkmarra, Coonjimba, Gulungul and Corndorl) are separated from the Magela Creek channel by low natural sand levees. Water may either flow from these lagoons over these natural levees into Magela Creek (the overflowing condition) or from Magela Creek

back into the lagoons (the backflowing condition). The direction of flow depends upon the relative flows in Magela Creek and the lagoon feeder streams.

The four main Magela Creek channel lagoons (Mudginberri, Buffalo, Mayamarleprard and Island) appear to be well flushed each year by the main creek flow. The time taken for these lagoons to overflow is dependent on the rate of inflow from the creek, vertical bank height above the water surface and the surface area of the lagoon.

The three floodplain lagoons studied (Leichhardt, Ja Ja and Jabiluka) lose their identity during the wet season as water from the Magela channel spreads over the plains and covers them. Leichhardt Lagoon is a depression on the western edge of the floodplain which received water from the main channel on 15.12.78. In some years this lagoon may receive runoff from local catchments, depending on the timing of rainfall in northern and southern sections of the Magela System.

METHODS

Observations on limnological conditions at the beginning of flow in the system were made between 25.11.78 and 22.12.78. The direction of flows between the lagoons and the creek channel were noted.

Water transparency was measured using a Secchi disc. Water samples were taken using a displacement sampler and then transferred to 250 ml glass bottles. Conductivity and pH were determined in the field using meters, from the water samples taken. Temperatures of bottom and surface water samples were measured using a thermometer. Dissolved oxygen was measured by the Winkler titration method.

Incidental observations on small isolated fish kills were noted in lagoons in the system in the course of routine fish sampling during a more extensive study of the biology and ecology of the freshwater fishes of the Alligator Rivers Region. Observations were made fortuitously on a major fish kill in Leichhardt Lagoon on 22.12.78.

The observations in Leichhardt Lagoon were restricted to the north-eastern end of the lagoon where the fish kill was most intense. The perimeter of the north-eastern end of the lagoon was divided into four zones (A, B, C and D — see Figure 3). Dead fish were counted and their lengths measured (either length to caudal fork (LCF), or total length (TL) for fish with rounded tails).

Zones A and B bordered the main waterbody and only dead fish within 4 m of the bank were recorded. Very few dead fish were seen floating in the middle of the lagoon. The density of dead fish observed in zones A and B appeared to be representative of the littoral zone of the entire lagoon, excluding a

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small backwater at the northern end of the main waterbody. Zones C and D encompassed this small backwater, which in the wet season functions as the lagoon overflow channel. All dead fish in zones C and D were recorded. All visible dead fish were eventually removed from zone D and then the entire area was seined using a 24 mm (knot to knot) mesh-sized seine net to check whether any dead fish had sunk or any fish had survived.

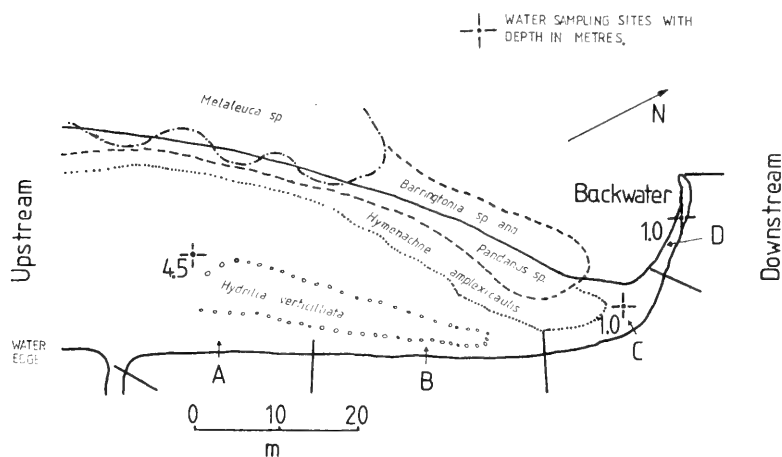


FIG. 3. Leichhardt Lagoon (22.12.78) showing fish kill zones, A, B, C and D, sampling sites and habitat details.

RESULTS

The rainfall at Jabiru (the township serving the Ranger mining operation) and the stream gauge height readings recorded at station GS 821-009 (on Magela Creek two kilometres downstream from Jabiru) during the period of the observations are shown in Figure 2.

START OF FLOW

Flow in Magela Creek was first observed on 25.11.78 at Georgetown Lagoon. On this day the flow front did not reach Mudginberri Lagoon but had begun to backflow into Georgetown and Djalkmarra Lagoons. The ensuing sequence of flushes caused by the floodpeaks on 25.11.78, and a later peak on 5.12.78 leading up to the observed fish kill in Leichhardt Lagoon, is shown in Table 1.

TABLE 1

THE SEQUENCE OF MAGELA CREEK LAGOON FLUSHES FOR THE START OF THE 1978/79 WET SEASON.

DATE	TIME	LOCATION	FLOW TYPE
25.11.78	1100	Georgetown (GN)	Backflowing
	1200	Djalkmarra (DA)	Backflowing
	1300	Magela Ck. near Coonjimba (CA)	All channels flowing
	1430	Magela Ck. near Gulungul (GL)	All channels flowing
	1500	Magela Ck. near Corndorl (CL)	Main channel flowing, side channel beginning to flow
	1600	Mudginberri (MI)	No inflow
	1730	Georgetown	Backflowing
	1800	Djalkmarra	Filled to creek level
26.11.78	1000	Georgetown	Filled to creek level
	1030	Magela Ck. near Georgetown	Level dropped by 20 cm.*
	1130	Djalkmarra	Overflowing
	1230	Magela Ck. near Coonjimba	Level dropped by 15 cm.
	1500	Magela Ck. near Gulungul	Level dropped by 10 cm.
	1600	Magela Ck. near Corndorl	Level dropped by 5 cm.
	1700	Buffalo (BO)	Inflowing only
27.11.78	1800	Georgetown	Slight overflow
	1900	Buffalo	Overflowing
29.11.78		Island (ID)	Inflowing
5.12.78	1400	Georgetown	Backflowing, floodpeak
6.12.78		Corndorl	Backflowing
7.12.78	1100	Coonjimba	Backflowing
7.12.78	1600	Gulungul	Backflowing
		Ja Ja (JJ)	Inflowing
15.12.78		Leichhardt (LT)	Beginning to inflow
21.12.78	1700	Leichhardt	Overflowing across floodplain, fish kill observed

* The drop in water level from peak flow on 26.11.78 was recorded by estimating vertical distance between the water level and the peak level contour on sandy banks.

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QUALITY OF FLOWING WATER

Table 2 lists some chemical and physical parameters of the flowing waters which were measured at a number of sites along Magela Creek. Changes in the parameters measured were apparent before, during and after flood peaks. pH is reduced in peak flows and then gradually increases towards pH 6.0 as the peak recedes. Secchi disc readings are reduced during the peaks, then gradually increase to over 1m. Conductivity was reduced during the floodpeaks on 5.12.78 and remained low. Temperature and dissolved oxygen were also reduced with this floodpeak but gradually increased as the flow subsided.

TABLE 2

QUALITY OF FLOWING WATERS IN MAGELA CREEK AT THE START OF THE 1978/79 WET SEASON

SITE: Magela Creek near**	MG	MD	GD	GD	MD	GD
DATE: December 1978	1	4	5*	7	8	8
TIME:	1645	1800	1630	1500	1710	1810
Secchi depth (cm)	50	120	20	100	120	100
pH	5.5	5.6	5.2	5.8	6.0	6.0
Conductivity (μ S/cm)	18.9	14.0	6.0	6.0	4.0	5.0
Temperature °C	30	34	31	34	35	35
Dissolved Oxygen (D.O.) (mg/l)	5.3	5.6	5.2	n.a.	5.6	5.6
Percentage saturation of D.O.	70	79	70	n.a.	80	80
Oxygen deficit (mg/l)	2.2	1.5	2.2	n.a.	1.4	1.4

*: Second floodpeak.

** : See Table 1 and Figure 1 for names and locations.

n.a.: Not available.

The physico-chemical character of flowing water would possibly be influenced by the presence of water in channel lagoons during the first few weeks of flow. Water flow into the channel lagoons would mix with lagoon waters and could also disturb bottom sediments (S. Clark, pers. comm.).

The backflowing lagoons would also affect the character of the creek, especially when floods recede. For example, on 3.12.78 Secchi disc readings were taken in a channel of Magela Creek just upstream of the overflow channel from Georgetown Lagoon, in this overflow channel, and in the Magela Creek channel just downstream of the overflow channel. The readings at these three sites were 60, 2 and 5 cm respectively, thus illustrating the influence of the Georgetown Lagoon overflow on the transparency of the creek waters downstream.

QUALITY OF LEICHHARDT LAGOON WATER

Chemical and physical water quality parameters in Leichhardt Lagoon before and during inflow conditions are shown in Tables 3 and 4. Observations made on 18.12.78 and 27.12.78 (Table 3) were taken in the middle of the main waterbody adjacent to zone A. Observations made on 22.12.78 (Table 4) were taken in the backwater (zones C and D, see Figure 3) where the fish kill was most intense.

TABLE 3
WATER QUALITY OF LEICHHARDT LAGOON

(a) DATE: 18.12.78 TIME: 1000 hrs. GAUGE HEIGHT: 3.02m						
Depth (m)	Temp. (°C)	Dissolved Oxygen (mg/l) (% Sat.) (deficit mg/l)			Conductivity (µS/cm)	pH
0.0	n.a.	n.a.	n.a.	n.a.	220	4.9
0.1	34.1	1.60	22	5.5	220	5.1
0.2	33.9	n.a.	n.a.	n.a.	n.a.	n.a.
0.5	33.6	1.90	26	5.3	210	5.3
1.0	33.4	1.50	21	5.7	210	5.4
2.0	33.2	1.00	14	6.2	210	5.3
3.0	32.8	0.67	9	6.6	230	4.55
4.0	32.4	n.a.	n.a.	n.a.	n.a.	n.a.
4.2	n.a.	0.60	8	6.7	255	4.0
4.5	32.6	n.a.	n.a.	n.a.	n.a.	n.a.
(b) DATE: 18.12.78 TIME: 1630 hrs. GAUGE HEIGHT: 3.02m						
0.0	n.a.	n.a.	n.a.	n.a.	220	3.9
0.1	33.4	5.70	79	1.5	200	3.95
0.5	33.5	4.80	67	2.4	195	4.5
1.0	32.8	3.10	43	4.1	195	5.25
2.0	32.1	0.86	12	6.5	190	5.25
3.0	31.6	0.63	9	6.7	210	4.7
4.0	31.4	n.a.	n.a.	n.a.	n.a.	n.a.
4.2	n.a.	0.22	3	7.2	220	3.9
4.5	31.1	n.a.	n.a.	n.a.	n.a.	n.a.
(c) DATE: 27.12.78 TIME: 1000 hrs. GAUGE HEIGHT: 3.12m						
0.0	n.a.	n.a.	n.a.	n.a.	210	4.4
0.1	30.7	2.23	30	5.2	210	4.4
0.2	30.7	n.a.	n.a.	n.a.	n.a.	n.a.
0.5	30.5	2.20	29	5.3	210	4.6
1.0	30.3	2.05	27	5.4	210	4.55
2.0	30.1	1.64	22	5.9	200	4.65
3.0	29.7	1.38	18	6.2	205	4.4
4.0	28.7	n.a.	n.a.	n.a.	n.a.	n.a.
4.3	n.a.	2.53	33	5.1	290	4.6
4.6	28.7	n.a.	n.a.	n.a.	n.a.	n.a.

n.a. — Not available.

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TABLE 4

WATER QUALITY OF LEICHHARDT LAGOON BACKWATER ON 21-22.12.78

DATE	21.12.78	22.12.78	22.12.78
TIME (hrs)	1700	0800	0800
ZONE	C	C	D
GAUGE HEIGHT (m)	3.06	3.06	3.06
SECCHI DEPTH (cm)	80	70	1
SURFACE:			
Temp. (°C)	38	35	34
Dissolved Oxygen			
(mg/l)	0.5	1.0	0.1
(% sat.)	7.5	14.0	1.0
(Deficit mg/l)	6.1	6.0	7.0
pH	—	4.0	5.4
Conductivity (µS/cm)	—	160	230
BOTTOM:			
Depth (m)	1.0	1.0	0.5
Temp. (°C)	37	35	34

In the main waterbody, dissolved oxygen levels were very low a few days before the observed fish kill. Considerable diurnal fluctuation in dissolved oxygen levels was observed on 18.12.78 (S. Clark, pers. comm.), the levels in surface waters increasing between 1000 hours (Table 3a) and 1630 hours (Table 3b), probably as a result of photosynthesis of aquatic plants in the lagoon. It was unfortunate that dissolved oxygen levels could not be measured (due to logistic constraints) in the early morning to see if surface waters became near anoxic at night. Conditions approaching anoxia persisted in the bottom waters on 18.12.78. Dissolved oxygen levels measured during inflow on 27.12.78 (Table 3c) were slightly elevated compared with those measured before inflow. Surface dissolved oxygen levels measured during the fish kill on 22.12.78 were extremely low (Table 4). In the backwater, zone D had the lowest surface dissolved oxygen and was highly turbid. Secchi disc readings in the backwater were lower than those in the main waterbody. Conductivity and pH varied only slightly in the main body of water before and during inflow. The highest conductivities were recorded from the bottom waters of the main waterbody on 18.12.78 and in zone D on 22.12.78. The pH ranges observed in zones C and D fell within the range of those observed in the main waterbody.

FISH KILLS

Details of fish kills observed prior to the kill in Leichhardt Lagoon are shown in Table 5. These kills were generally very small, with the largest occurring in

Jabiluka, Ja Ja and Mayamarleprard Lagoons. *Lates calcarifer* dominated most kills. All kills except one (Magela Creek near Georgetown Lagoon) occurred in the lower reaches of the creek. The kill in Magela Creek near Georgetown Lagoon occurred in a branch of the creek which dried up into a series of isolated sandy pools after the 25.11.78 peak flow had subsided.

TABLE 5
SUMMARY OF FISH KILLS OBSERVED IN THE MAGELA CREEK CATCHMENT
FOR 1978 DRY SEASON

DATE	LOCATION	SPECIES	APPROXIMATE NUMBERS OF FISH
21.9.78	Island	<i>Lates calcarifer</i>	1
10.10.78	Mayamarleprard	<i>Lates calcarifer</i>	10
20.11.78	Jabiluka	<i>Lates calcarifer</i>	10
20.11.78	Jabiluka	<i>Hexanematichthys leptaspis</i>	5
22.11.78	Ja Ja	<i>Lates calcarifer</i>	20
25.11.78	Mudginberri	<i>Lates calcarifer</i>	3
1.12.78	Magela Ck. near Georgetown	<i>Leiopotherapon unicolor</i>	Occasional dead fish
7.12.78	Buffalo	<i>Lates calcarifer</i>	" " "
11.12.78	Island	<i>Hexanematichthys leptaspis</i>	" " "
22.12.78	Leichhardt	see Table 6.	

LEICHHARDT LAGOON FISH KILL

The main features of the habitat in the zones in Leichhardt Lagoon where the fish kill was most intense are shown in Figure 2.

A list of fish species killed and their abundances in the four zones of Leichhardt Lagoon are given in Table 6. Eight species of fish were observed in the kill, and six of these (*Lates calcarifer* to *Strongylura krefftii* in Table 6) had lengths greater than 18 cm. (Figure 4). *Liza diadema* was the most abundant large fish species killed. *Ambassis agrammus* and *Glossamia aprion* were the only small fish species killed. Anuran larvae and hemipterans (*Agraptocorixa* spp.) were also observed dying.

The densities of "large" (length > 18 cm) fish killed per metre of stream bank in the four zones are given in Table 6. The lowest densities of dead fish were in zones A and B. If the density (0.14 fish/m) of dead large fish in these zones is assumed to be representative of the total perimeter (2.1 km) of the lagoon, then the total number of dead large fish in the lagoon (excluding zones C and D) would have been approximately 305. The highest density of dead fish was observed in zone D followed by zone C.

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TABLE 6

DETAILS OF FISH KILL OBSERVED IN LEICHHARDT LAGOON ON 22.12.78

FISH SPECIES	FISH KILL ZONES ^A				TOTAL NUMBERS
	A	B	C	D	
Silver barramundi <i>Lates calcarifer</i>	2	7	14	4	27
Ord River mullet <i>Liza diadema</i>	16	24	86	72	198
Forktailed catfish <i>Hexanematichthys leptaspis</i>	2	4	17	3	27
Eeltailed catfish <i>Neosilurus</i> sp.A (yellow bellied)	4	4	13	2	23
Bony bream <i>Nematalosa erebi</i>	4	1	1	0	6
Freshwater longtom <i>Strongylura krefftii</i>	1	1	0	0	2
Chanda perchlet* <i>Ambassis agrammus</i>	0	0	0	c.100*	c.100*
Mouth almighty <i>Glossamia aprion</i>	0	1	0	0	1
TOTAL NUMBERS OF LARGE FISH (EXCLUDING*)	29	41	141	81	284
KILL DENSITY (N/m of bank)	0.12	0.17	0.35	1.35	

N/m = Numbers of dead fish observed per metre of bank.

^A = See Figure 3.

Between 100 and 200 *Liza diadema* and 10 and 20 *Lates calcarifer* were observed swimming in zones B and C, gulping for air and 'scooping' a thin layer of surface water.

Postmortems were conducted on ten specimens of each species and the most noticeable feature was the reddened gills of both species (i.e. their gills were engorged with blood). The air-gulping behaviour observed is a characteristic reaction of fish to low dissolved oxygen levels (Odum and Caldwell, 1955). However, the reddened gills of the fish indicated that blood contained therein appeared to be saturated with oxygen, thus suggesting a physiological inability to take up oxygen into body tissues.

The length frequencies of the most common larger fish species are shown in Figure 4. The dead *Liza diadema* ranged in length from 30 to 57 cm and live specimens collected by seine net in zone D ranged in size from 23 to 45 cm. These live seine net specimens occurred in two size groups; the individuals from the smallest group were smaller than all *L. diadema* observed in the kill and the

second group was similar in size to the size class of the majority of *L. diadema* which had died. The smallest size class of *L. diadema* may not have appeared in the fish kill because they were not affected by the environmental conditions lethal to larger fish and/or this small size group may have been affected but were removed by scavengers more rapidly due to their size. Few small fish were found in the kill though many small species *Melanotaenia maculata*, *Hypseleotris compressus*, *Denariusa bandata* and *Neosilurus* sp.C (yellow finned colour type) are known to occur abundantly in the area judging from previous seine net samples taken by the author a week beforehand in the littoral zone of this lagoon. Large numbers ($n = 40$) of white breasted sea eagles (*Haliaeetus leucogaster*) and whistling kites (*Haliastur sphenurus*) were observed feeding on fish carcasses located on the banks of the lagoon. *Toxotes chatareus* (archerfish) and *Megalops cyprinoides* (tarpon) are also known to occur abundantly in the lagoon from previous gillnet samplings but were not present in the kill.

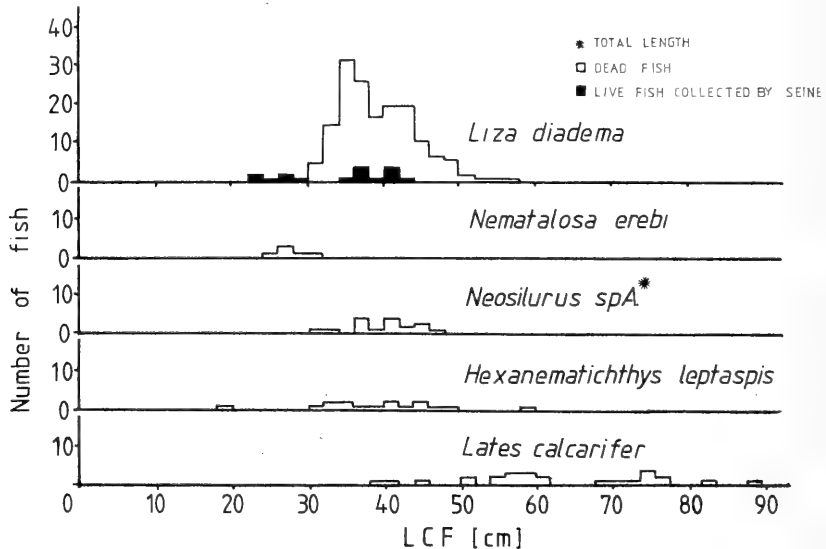


FIG. 4. Length frequency distributions of the most common larger fish species present in the Leichhardt Lagoon fish kill. LCF = Length to caudal fork.

DISCUSSION

Fish kills in the Magela Creek catchment have been frequently observed by local residents following the beginning of the wet season, i.e. October to December. Giles (1974) noted minor fish kills in Magela Creek lagoons during the last month of the dry season in 1973. Giles speculated that populations of fish in Magela Creek were stressed by a number of factors which included high

water temperatures, reduced dissolved oxygen (due to increased temperature), lowered water levels, low pH and increases in dissolved heavy metals, all of which increase their susceptibility to disease as a result of stress. The Ranger Uranium Environmental Inquiry (Fox) Second Report (Commonwealth of Australia 1977) indicated that the factors responsible for fish deaths in the Region are not known, that there is a general paucity of information about the complex aquatic systems, and that specific data for the Magela system were very limited.

The physical and chemical condition of the flowing waters recorded in Table 2 did not appear to affect the fish within the upper reaches of the Magela Creek. The parameter limiting fish life in Leichhardt Lagoon on 22.12.78 appeared to be dissolved oxygen; this assumption is supported by observations on the air gulping behaviour of fish in the most intense fish kill zones. Dissolved oxygen levels in Leichhardt Lagoon before inflow commenced were extremely low, especially in the bottom waters. However, after inflow commenced conditions appeared to deteriorate in surface waters (probably as a result of mixing of both waters caused by either inflow or winds), particularly in the recently inundated shallow backwater where the fish kill was most intense. It is unknown why dissolved oxygen levels were further reduced in the backwater compared with the main waterbody after inflow: however, the input of biologically active sediments with the inflowing waters, plus the effect of large numbers of fish congregating in the recently inundated backwater, stirring up organic rich muds into suspension, may have been the cause. Why the fish congregate in near anoxic backwater is unclear, especially as some fish populations are known to evade the consequences of lowered dissolved oxygen (Mosevich, 1947). However, *Lates calcarifer* (Reynolds, 1978) and probably *Liza diadema* (Roberts, 1978) are catadromous species which undertake downstream migrations to estuarine waters as part of their life cycles. The backwater where the fish were congregating is the overflow channel connecting the lagoon towards the estuarine reaches during most of the wet season.

Mechanisms causing fish mortalities which are similar to that proposed above have been recorded in tropical South America by a number of authors. Geisler and Freiburg (1969) noted that fish mortalities occur in the lower reaches of the Rio Negro, a typical Amazonian 'blackwater' river, during periods of strong winds. Observations on stratification in a slow-flowing stretch of the river showed that death was due to the upwelling of anoxic bottom waters. Most species of fish tested by Geisler and Freiburg in the laboratory were found to require at least 0.75-1.0 mg/l of dissolved oxygen for survival. Infante *et al.* (1979) recorded mass fish mortalities in Lake Valencia, Venezuela, resulting from similar changing environmental conditions to those recorded by Geisler and Freiburg. Bottom waters in the lake were anoxic and contained large amounts of reducing substances during calm conditions; after winds commenced, complete mixing occurred resulting in surface waters having reduced dissolved oxygen levels and increased levels of hydrogen sulfide, ammonia and nitrite. De Menezes Santos

(1979) made limnological observations on the asphyxia of Central Amazonian fishes from the lakes of the Janauaca Region of Brazil. The oxidation of material brought to the lakes by flooding tended to reduce the dissolved oxygen level to zero in the hypolimnion. This phenomenon caused the fish to come to the surface (behaviour known as 'aiu' in that Region). Again, persistent winds causing mixing of bottom and surface waters caused symptoms of asphyxia and death of some fish species.

The common mechanism for the above fish mortalities was the mixing of bottom anoxic waters (caused by either winds and/or floods, and in the latter example aggravated by the oxidation of material brought in by floods) mixing with surface waters resulting in lowered oxygen levels throughout the waterbodies.

Two observations made during the Leichhardt Lagoon fish kill tend to indicate that low dissolved oxygen concentrations was not the only factor which caused the observed mortalities. The reddened gills of the fish congregating in the most intense fish kill zones indicate the possibility of a physiological mechanism inhibiting uptake of oxygen into body tissues from blood. The occurrence of *Agraptocorixa* spp. in the kill is puzzling as these corixids utilize atmospheric oxygen (Williams, 1968).

The freshwater mangrove (*Barringtonia acutangula*) is a plant species which is abundant upstream of and within Leichhardt Lagoon; Harmer (1976) noted that aborigines use all parts of this tree as a fish poison in the Region. The effects on the fish fauna of potentially toxic compounds released from these plants during the inflow period is unknown.

Examples of minor to moderate man-induced fish kills have been observed by Jeffree and Williams (1975) in the upper reaches of the Finniss River, also in the tropical area of the Northern Territory. These fish kills were associated with the entry of heavy metal pollutants, mainly copper and zinc, from the abandoned Rum Jungle uranium mining area. The kills occurred at the beginning of each wet season whenever a flush through the eastern branch of the Finniss River (on which the Rum Jungle project was located) did not coincide with a high flow in the Finniss River channel, and provided that the fish populations had been able to recolonise from adjacent unpolluted zones. Jeffree and Williams recorded the following fish genera in the above kills: *Ambassis*, *Craterocephalus*, *Glossamia*, *Glossogobius*, *Leiopotherapon*, *Megalops*, *Melanotaenia*, *Mogurnda*, *Neosilurus*, *Oxyeleotris* and *Strongylura*.

Since the present study was completed a large fish kill was observed at the beginning of the 1979/80 wet season (3-8.1.80). This fish kill occurred in Ja Ja Lagoon after it had received some runoff from surrounding catchments but before the Magela Creek had commenced to flow across the flood plain. No other significant fish kills were observed to have occurred in the Magela flood plain during

FISH KILLS EAST ALLIGATOR RIVER

this period. A total of some 2500 specimens belonging to at least 10 species, including some 400 *Lates calcarifer*, were involved in the kill (H. Midgley, pers. comm.). The high mortalities of *L. calcarifer* noted have implications for fisheries management in relation to such lagoon habitats. Once lagoons can be identified which may have high *L. calcarifer* mortalities, then amateur fishing restrictions should be lifted so that fishermen may take fish which would presumably otherwise die and be replaced by migration into the lagoon system at the beginning of the following wet season.

CONCLUSIONS

The limited data on northern Australian tropical freshwaters suggest that low dissolved oxygen levels (lowered by the mixing of anoxic bottom waters) may explain the observed fish kill in Leichhardt Lagoon; however, some observations indicated that low dissolved oxygen concentration may not have been the only factor which caused the mortalities. Distinguishing between man-induced and natural fish kills is very difficult owing to our scant knowledge of factors and mechanisms which affect fish survival in such waters.

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Mosquitoes (*Mimomyia elegans* (Taylor)) Feeding on the Introduced Toad *Bufo marinus* (Linnaeus): Implications for Control of a Toad Pest

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ABSTRACT

The mosquito *Mimomyia elegans* (Taylor) was observed to feed on the introduced toad *Bufo marinus* near the toads' present southern limit of distribution in Australia. Since mosquitoes are vectors for a number of infectious diseases of anurans a search for mosquito-borne diseases of *B. marinus* might provide information for selective control of a toad which is considered harmful to native wildlife.

INTRODUCTION

Bufo marinus was introduced into Australia in 1935 in the hope that it would control certain coleopteran pests of sugar cane (Tyler, 1976). Since then there has been considerable debate concerning the relative benefit and detriment of the toad in view of its effects on the native fauna of areas into which it has spread (van Beurden, 1978). *B. marinus* has been demonstrated to be highly toxic to some native vertebrates and ineffective in controlling target beetle pests with which it rarely comes in contact (Covacevich and Archer, 1975).

Because *B. marinus* is spreading rapidly into new areas (van Beurden and Grigg, 1979) it would be desirable to develop an effective and specific means of control. Heatwole and Shine (1976) suggested the possibility of disease transmittance by mosquitoes as a control measure.

This paper reports on an observation on mosquitoes feeding on toads and the possible implications for control.

OBSERVATIONS

On a dry evening (2200 hrs on the 3rd February, 1979) when carrying out a mark-recapture programme, toads were observed on a sealed road surface at Lennox Head near Byron Bay, New South Wales. The southern limit of distri-

bution of these toads in Australia is about 10 kilometres south of this road. The road traverses undulating grazing pastures and is bordered by dense grass up to one metre in height. A row of She-oaks (*Casuarina* sp.) up to three metres in height runs parallel to the road 5 metres from either edge. The road terminates in mangrove swamp about 100 metres past the collection area. Out of eight adult toads observed (length > 60 mm), five had mosquitoes either feeding on them or walking over them. One female toad had a mosquito perched on the posterior edge of each naris. Both mosquitoes had their probosces inserted into the narial epithelium. All mosquitoes, once they had settled, commenced feeding and remained on the toad until turgid. In no case was there evidence that the toads were irritated. These mosquitoes were identified as *Mimomyia elegans* (Taylor). Three further toads, originally free of mosquitoes, were invaded when they hopped under the grass canopy at the edge of the road.

DISCUSSION

A number of species of mosquito have been reported to feed on anurans (Woke, 1937; Causey, 1939; Remington, 1945; Marks, 1960; Gillett, 1971; Heatwole and Shine, 1976). Marks (1960) noted that *Uranotaenia albescens* and *Culex* (*Lophoceraomyia*) spp. might transmit haemogregarine parasites when feeding on *Litoria caerulea*. Experiments with *Culex molestus* demonstrated that this species successfully transmits parasitic filaroid nematodes found in *Rana ridibunda* (Wittenburg and Richter, 1954). *Anopheles maculipennis* transmits a lung fluke (Trematoda) from snails to frogs, presumably, when adult mosquitoes (infected during the larval stage) are ingested by the frog (Gillett, 1971). No mosquito has previously been reported feeding on *Bufo marinus*. *Culex annulirostris*, *C. fatigans*, *C. (Lophoceraomyia)* spp. and *Uranotaenia albescens* were found to contain blood meals from amphibians in areas where *Bufo marinus* was abundant (Kay *et al.*, 1979).

M. elegans occurs in Australia, Sumatra, Malaya, Bismarck Archipelago, New Guinea, Philippines, Thailand and Ryukyu Islands (Knight and Stone, 1977). This species occurred throughout coastal Queensland (Marks pers. comm.) and inland at Charleville (Kay, 1979). Taylor (1929) found larvae at the edge of a swamp in cattle hoof prints containing decaying vegetable matter, these larvae were associated with larvae of *M. chamberlaini* var *metallica* (Leicester). Adults have been found resting amongst dense grass or water hyacinth (*Eichornia*) in swampy areas (Marks pers. comm.).

Little is known of diseases specific to *Bufo marinus*, although 7 species of salmonella (Kournay *et al.*, 1970) and four protozoan parasites have been reported from them. The protozoans are (1) the myxosporidian *Cystodiscus immersus*, (2) the gut balantidium *Nosema balantidii* (Reichenbach-Klinke and Elkan, 1965), (3) the blood rhizopod *Cytoamoeba bactipera* (Lehmann, 1966) and (4) the gut

flagellate *Tritrichomonas batrachorum* (Markinelle, 1968). Of these protozoans only *Cytoamoeba bactipera* and *Cystodiscus immersus* are potentially lethal and only the former might be transmitted by mosquitoes. Seven helminth parasites are reported also (see Zug and Zug, 1979) but only the microfilaria *Ochoterenella* cf. *digicauda* (Markinelle, 1970) are potentially transmissible by mosquitoes.

The information regarding diseases of *Bufo marinus* reflects a lack of detailed investigation rather than indicating that they are all characteristically healthy. More intensely studied toads such as *Bufo bufo* are known to be prone to a broad range of infectious diseases (see review by Elkan, 1960). Haemolytic pseudomonads (Dusi, 1949), haemolytic sporozoans (e.g. *Plasmodium bufonis* Fantham, et al., 1942) and myolytic sporozoans (e.g. *Plistophora bufonis* Guyenot and Ponse, 1926 and *P. myotrophic* Elkan, 1960) occur in toads and together with gregarines and nematodes all appear to be suitable for transmittance by mosquitoes. Discovery in Central America of a mosquito-borne disease specific to *Bufo marinus* would stimulate studies on the receptivity of Australian anurans to the disease and also of the potential of *M. elegans* and other Australian mosquitoes to act as vectors. The possibility of looking for a disease from other countries is again faced with the problems of introducing yet another species, an unknown quantity, into the Australian environment.

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NOTICE TO AUTHORS

Papers will be considered for publication in *The Australian Zoologist* if they make an original contribution to whole animal biology of the Australian fauna. Papers submitted will be subjected to review and thence to the normal editorial process, in the course of which authors will receive edited galley proofs for correction. A manuscript is accepted on the understanding that it is to be published exclusively in *The Australian Zoologist*.

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The abstract (up to 200 words) should state concisely the scope of the work and the principal findings and should be suitable for direct use by abstracting journals. The section headings should be Introduction, Materials and Methods, Results, Discussion, Acknowledgements and References. Presentation must be clear and concise and all unnecessary repetition especially in consecutive sections should be avoided. Footnotes should be avoided.

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ILLUSTRATIONS AND DIAGRAMS should be larger than the size of the finished block. Drawings must not exceed 30 x 20 cm. If the originals exceed this they should be photographically reduced and good quality prints provided. Half tone prints should be arranged as plates and mounted on stiff white board up to a maximum size of 30 x 20 cm. Authors will be allowed up to two plates free of charge, but will be expected to pay the cost of any additional plates.

SHORT PAPERS these should be no more than six typewritten pages long and should deal with a technique experiment or important observation not reaching lengthy treatment. Isolated factual notes would not be considered suitable.

Two new generic names for some Australian pufferfishes (Tetraodontiformes: Tetraodontidae), with species' redescriptions and osteological comparisons

GRAHAM S. HARDY

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ABSTRACT

Marilyna n. gen. is proposed for three Australian pufferfish species, *M. pleurosticta* (Günther), *M. meraukensis* (de Beaufort), and *M. darwinii* (Castelnau). *M. meraukensis* is recorded extensively from Australia for the first time, and *M. darwinii*, long ignored by ichthyologists is confirmed as a valid, applicable name.

Marilyna is characterised by a broad, heavily built body, eyes set below the dorsal profile, nasal organ with two openings, eye rim completely adnate, a large olfactory foramen in each prefrontal, and a deep caudal peduncle.

Reicheltia n. gen. is proposed for the single species *R. halsteadi* (Whitley). It differs from *Marilyna* in the lighter built, narrower body, eyes interrupting the dorsal profile, a small olfactory foramen in each prefrontal, and a shallow caudal peduncle.

INTRODUCTION

The Australian pufferfishes have long been subject to taxonomic confusion. Ongoing studies have disclosed not only several formerly unrecognised species, but also several inadequacies in the generic allocations of previously described species (see also Hardy, 1980, 1981a, b; Hardy & Hutchins, 1981).

The Australian species possessing a nasal organ with two nostrils (as opposed to single or double nasal flaps), can be separated into a number of readily recognisable (generic) groups, characterised by considerable endemism. Such separation can be made almost wholly on morphological grounds and is confirmed by examination of osteological features. Accordingly, *Torquigener* Whitley, presently under revision, is distinct from all other related Australian genera in having the ventral rim of the eye infolded (i.e. eye rim dorsally adnate only). The species considered in this paper differ from *Contusus* species by the presence of a ventrolateral skinfold (Hardy, 1981b). However, because the habit of previous workers has been to arbitrarily include many Australian species under

"catch-all" generic names, it has been found necessary to introduce two new generic names, one for *Sphaeroides halsteadi* Whitley, and one for *Sphaeroides meraukensis* de Beaufort, *Tetrodon pleurostictus* Günther and *T. darwinii* Castelnau. All four species have been hitherto poorly known; indeed *T. darwinii* has been all but completely ignored for nearly 100 years, with a synonymous name for the species (*T. fasciatus* MacLeay) being included under *T. pleurostictus* for over 50 years, despite gross morphological and osteological differences.

METHODS AND ABBREVIATIONS

Measurements were taken by dial caliper and millimetre rule (to the nearest 0.1 mm for dimensions less than 10 mm), in a manner similar to that outlined by Dekkers (1975). All measurements are from preserved specimens. Fin ray counts include all visible rays, both branched and unbranched, and fin ray lengths were determined by measurement from the embedded base. One example of each species was cleared and stained; 60 specimens in total were X-rayed, for examination of their osteology.

The following abbreviations are used in the text:

SL,	standard length;
TL,	total length;
HL,	head length;
n,	number of specimens examined;
m,	depth in metres (precedes specimen registration number in lists of material examined);
AMS,	Australian Museum, Sydney;
ANSP,	Academy of Natural Sciences, Philadelphia;
BMNH,	British Museum (Natural History), London;
CSIRO,	Commonwealth Scientific and Industrial Research Organisation, Fisheries & Oceanography Division, Cronulla;
MNHN,	Muséum National d'Histoire Naturelle, Paris;
NMNZ,	National Museum of New Zealand, Wellington;
NTFD,	Northern Territories Fisheries Division, Darwin;
QM,	Queensland Museum, Brisbane;
WAM,	Western Australian Museum, Perth;
ZMA,	Zoological Museum, Amsterdam.

DESCRIPTIONS

Marilyna n.gen.

Type species: *Tetrodon pleurostictus* Günther, 1872:653, 674, pl.69A.

DIAGNOSIS

A genus of tetraodontid fishes with the following combination of characters: broad, heavily-built body; nasal organ with two unequally sized openings; eye

NEW GENERIC NAMES FOR AUSTRALIAN PUFFERFISHES

rim completely adnate; top of pectoral fin base above lower margin of eye; weak ventrolateral skin fold present on caudal peduncle; deep caudal peduncle (least depth $< 9.5 \times$ in SL); prefrontals large and broadly rounded, each with an extensive olfactory foramen, and in broad contact with palatine; frontals wide over orbit; sphenotic in contact with supraoccipital.

ETYMOLOGY

The genus is named after my wife Marilyn, who spared no efforts in bibliographic research throughout my studies on Australian tetraodontids, and who assisted uncomplainingly at poison stations in the hot, muddy, and potentially dangerous mangrove swamps of North Queensland.

REMARKS

There has been little pattern in the history of generic allocation of *Marilyna* species. *Tetraodon* (or *Tetrodon*) has often been used for *fasciatus* (junior synonym of *T. darwinii* Castelnau) and *pleurosticta*, and *Sphoeroides* (or *Sphaeroides* or *Spheroides*) for *pleurosticta* and *meraukensis*. It is now quite clear following the works of Shipp (1974), Dekkers (1975), and Tyler (1980), that *Tetraodon* and *Sphoeroides* are inadmissible generic names for the above species.

Fraser-Brunner (1943) referred *pleurosticta* (as *pleurostictus*) to *Torquigener* and has been followed in this respect by Munro (1956), Tyler (1970, 1980), and Tyler and Paxton (1979). However, Munro (1967) referred *pleurosticta*

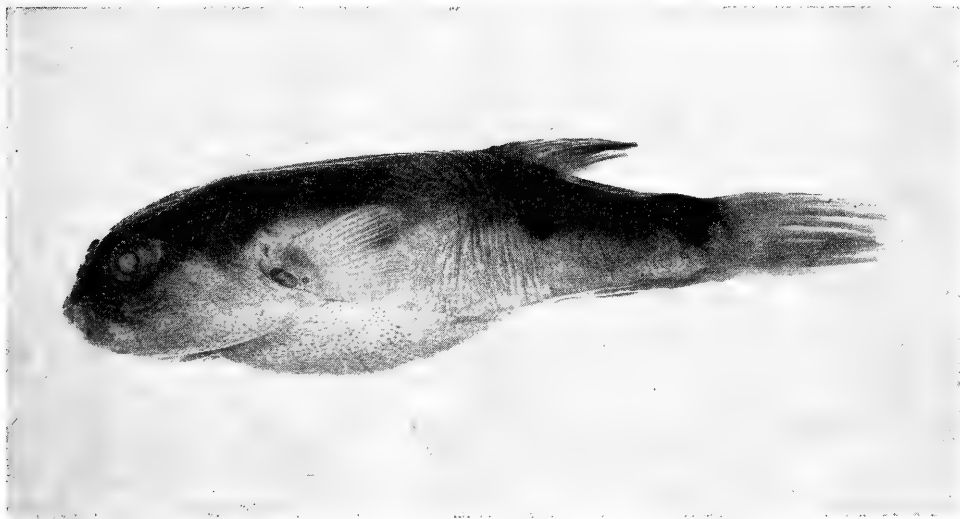


Fig. 1a. *Marilyna pleurosticta*

Lectotype, BMNH 1871. 9. 13. 128, 82 mm SL.

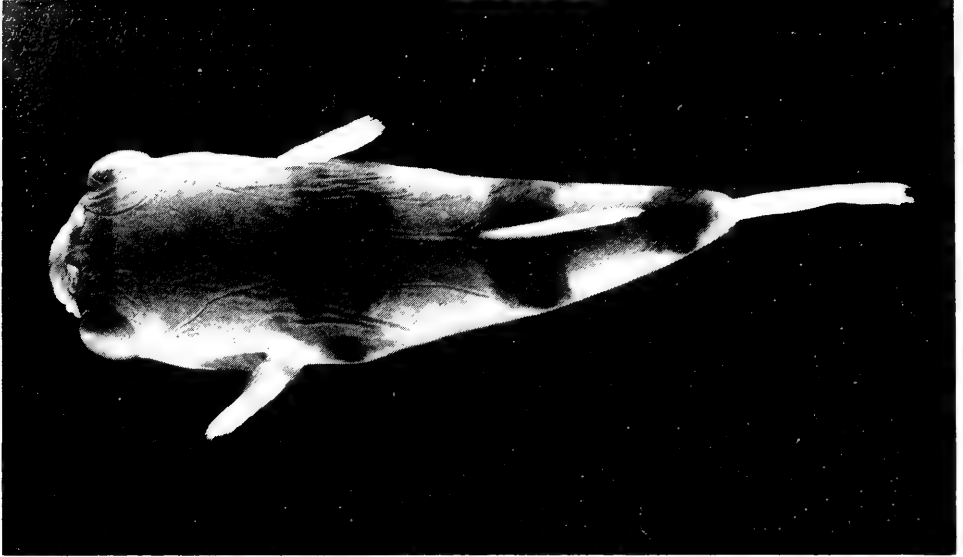


Fig. 1b. *Marilyna pleurosticta*
NMNZ P. 10166, 79mm SL dorsal view.

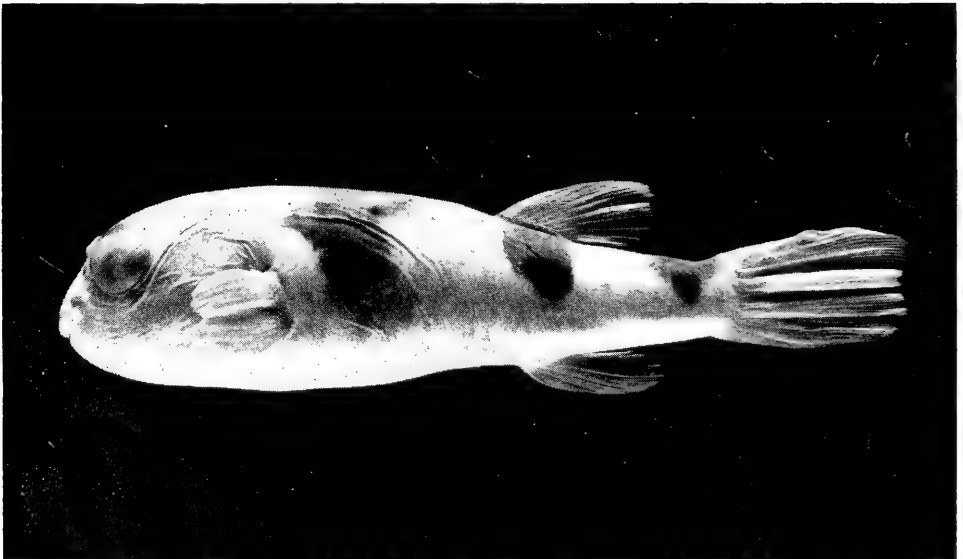


Fig. 1c. *Marilyna pleurosticta*
NMNZ P. 10166, 79 mm SL, lateral view.

(as *pleurostictus*) (a misidentification of *darwinii*) without comment to *Torafugu* Abe, 1939, and *meraukensis* to *Takifugu* Abe, 1949. Both generic names were originally proposed by Abe at the subgeneric level. My examination of examples of species referred to these subgeneric names by Abe (1939, 1949, 1952), shows them to be generically distinct from *Marilyna* species, differing amongst other features, in eye rim structure. Whitley's (1965) inclusion of *pleurostictus* in *Gastrophysus* was unexplained.

***Marilyna pleurosticta* (Günther, 1872)**

(Figs. 1A, B, C; 5A)

Tetrodon pleurostictus Günther, 1872, 653, 674, pl. 69A; MacLeay, 1881, 276; ———, 1882, 340; Regan, 1903, 302 (part); Günther, 1910, 463; de Beaufort, 1955, 54; ———, 1962, 383; Tyler, 1964, 128.

Tetrodon bibroni Castelnau, 1878, 247; MacLeay, 1881, 276; ———, 1882, 340; Stead, 1907, 27; McCulloch & Whitley, 1925, 178.

Tetrodon laevis de Vis, 1884, 456.

Sphaeroides laevis. Jordan & Seale, 1906, 368.

Sphaeroides pleurostictus. Stead, 1907, 27; Kabata, 1968, 519.

Tetrodon bibronii. McCulloch & Whitley, 1925, 178.

Sphaeroides pleurostictus. McCulloch & Whitley, 1925, 178; McCulloch, 1927, 103; ———, 1929-30, 431 (part); Marshall, 1964, 493-4, colour pl. 70 (part); ———, 1966, 221, colour pl. 70 (part); Thomson, 1977, 63.

Sphaeroides pleurostictus. Fowler, 1928, 468 (part); de Beaufort, 1962, 376, 382-3 (part).

Torquigener pleurostictus. Fraser-Brunner, 1943, 11 (part); Tyler, 1970, 22; ———, 1980, 291, 330, 331, Fig. 215, 267, Table 2; ——— & Paxton, 1979, 22.

Colomesus fasciatus (not of Bloch & Schneider). Le Danois, 1959, 211, 246, 253, 255, Fig. 177-178 (part); Tyler, 1964, 127 (part).

Gastrophysus pleurostictus. Whitley, 1965, 59 (part); Carcasson, 1977, 275.

Sphaeroides (= *Torafugu*) *pleurostictus*. Grant, 1978, 617, colour pl. 273 (part).

DIAGNOSIS

Marilyna with spines present only as a dense patch on belly, extending from level with posterior margin of eyes to level with posterior of pectoral fin margin. Four broad, dark bands cross body, posteriormost band on distal portion of caudal peduncle.

Prefrontals somewhat triangular in outline, with moderately large olfactory nerve foramina. Sphenotic wings laterally produced. Small but distinct triturating teeth on upper jaw.

DESCRIPTION

The following meristic counts and proportions are for the lectotype (82 mm SL), and, in parenthesis, are the range for the paralectotype and 22 non-type specimens (72-131 mm SL).

Dorsal rays 11 (9-11); anal rays 8 (8-9); pectoral rays 16-17 (16-18); caudal rays 11 (11); vertebrae 8 + 11 (8 + 10, 8 + 11, 9 + 11, 8 + 12, 8 + 13).

Body robust, broadly rounded dorsally and flattened ventrally, elongate, tapering to a deep caudal peduncle. Head length 3.1 (3.0-3.1) in SL; snout to anterior of vent 1.6 (1.5-1.6) in SL; to origin of dorsal fin 1.5 (1.5-1.6) in SL; to origin of anal fin 1.4 (1.4-1.5) in SL; to origin of pectoral fin 2.7 (2.7-3.0) in SL; body width at base of pectoral fin 3.3 (2.9-3.7) in SL; depth from dorsal fin origin to anal fin origin 4.1 (4.0-4.8) in SL; body depth at posterior end of dorsal fin base 5.9 (5.6-6.4) in SL; caudal peduncle length 4.3 (4.3-4.9) in SL; least depth of caudal peduncle 8.3 (8.3-9.2) in SL.

Mouth small and terminal on a moderately short snout, width 3.0 (2.5-3.4) in HL. Lips thick, covered with numerous short papillae. Chin lacking. Nasal organ a short papilla just forward of eye, with 2 widely separated openings, the posterior one larger; inner surface of papilla with a large fold sited posteriorly on medial portion and about 4 smaller folds sited posteriorly on the ventral portion. Snout to anterior edge of nasal organ 3.3 (2.6-3.4) in HL; posterior edge of nasal organ to anterior edge of eye 6.5 (6.4-7.7) in HL.

Eye round, moderate in size and rim completely adnate, with the upper border just below dorsal profile, and the lower border just above level of mouth corner; horizontal diameter 4.1 (3.5-4.5) in HL. Anterior edge of gill opening smooth. Posterior of eye to dorsal corner of gill opening 2.2 (1.9-2.4) in HL.

Pectoral fin margins rounded; 1st ray very short; maximum length of fin from base 6.1 (6.2-7.2) in SL; top of fin base above lower margin of eye. Dorsal fin located posterior to vent, fails to reach caudal fin base, distal margin bluntly pointed; 1st ray 24.1 (10.6-26.5) in SL; longest ray 5.1 (4.9-5.8) in SL; base length 8.7 (8.6-10.7) in SL and 1.7 (1.6-2.0) in longest ray. Anal fin base below posterior half of dorsal fin base; distal margin bluntly pointed and fails to reach caudal fin base; 1st ray 15.2 (10.2-19.8) in SL; longest ray 5.7 (5.4-6.1) in SL; base length 13.9 (13.3-16.2) in SL and 2.5 (2.3-2.8) in longest ray. Caudal fin truncate; maximum length 4.3 (3.8-4.9) in SL.

Ventrolateral skinfold extending from behind pectoral fin to caudal fin. Lateral line fairly distinct, encircling eye with a pre-opercular branch dropping to anterolateral limit of belly, running dorsolaterally along body towards caudal fin, rising over pectoral fin and gently dropping to lateral surface in region of dorsal fin; dorsolateral branches of lateral line above pectoral fin base and anterodorsal branches anterior to nasal papillae both meeting in middle; second lateral line dropping from behind mouth corner, extending along lateral region of belly and curving almost to pectoral fin base, continuing along belly from

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posterior limit of belly spines, medial to ventrolateral skinfold, almost to caudal fin. Body spines multi-rooted, and restricted to a dense arrangement on belly, extending from level of eye to posterior margin of pectoral fin.

Colour in alcohol (lectotype): dorsum dark brown; slightly darker bands cross interorbital and mid-dorsal regions; darkish patch at dorsal and caudal fin bases; lateral surface becoming pale, with dark spots at posterior of pectoral fin margin and beneath dorsal fin base. Belly and fins pale.

Colour in life (based on underwater observations): ground colour of dorsum and dorso-lateral surface pale olive-green to dark greenish-grey; dark bands, either solid or composed of irregularly distributed round spots, cross dorsum at eyes, mid-dorsum, dorsal fin base, and distal end of caudal peduncle; these bands either extend almost to ventro-lateral region, or remain distinct from moderate to large, dark, lateral blotches; ventro-lateral surface pale or with silverish sheen; belly and chin white; pectoral and dorsal fins tinged reddish to reddish-yellow; anal fin bright orange to yellow; caudal fin reddish-yellow, becoming bright orange distally.

DISTRIBUTION

It is recorded only from the Australian east coast, from Cooktown, North Queensland, to Smith's Lake, N.S.W., and is a shallow water, predominantly estuarine species.

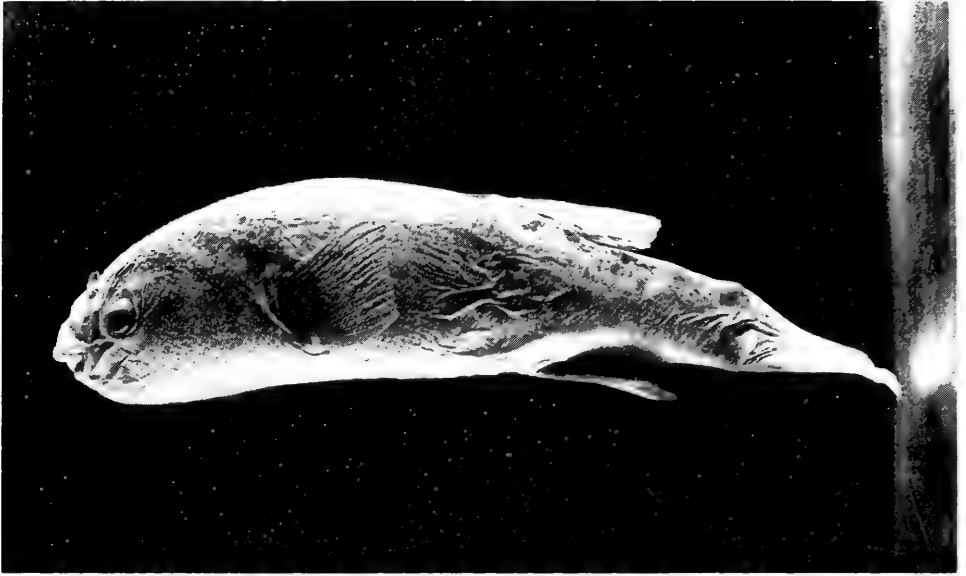
REMARKS

Recognition of Günther's (1872) type specimens of *Tetrodon pleurostictus* is straight forward and there is no direct indication that he had further material at hand. However, his description of *pleurostictus* referred to the species sometimes having minute dorsal spines. Such a feature is missing on the syntypes, and has not been found in any example of the species. Accordingly one must conclude that Günther had examined further specifically distinct material, which he mistakenly included in *pleurostictus*. Nonetheless, the identity of the types (BMNH 1871. 9.13.128 here designated as lectotype) fixes the use of the name *pleurosticta* for the species concerned.

I have not been able to locate type material of *Tetrodon bibroni* Castelnau and *T. laevis* de Vis. Although the descriptions are brief, the colour patterns and spine distributions given for these species are consistent with that of *pleurosticta*.

De Beaufort (1962) and Munro (1967) clearly confused *pleurosticta* with *fasciatus* (= *darwinii*), in referring to dorsal spination, and whilst the former author recognised that some problems existed in species identity, he failed to resolve them.

Fig. 2. *Marilyna meraukensis*



A. Lectotype, ZMA 104. 139, 196 mm SL.



B. WAM unreg., 76 mm SL.

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Tyler (1980, fig. 215) illustrated the lateral lines and nasal organ of this species, which he called *Torquigener pleurostictus*.

SPECIMENS EXAMINED

(n = 47; 2 or more specimens in a lot is indicated by a number in parenthesis).

Lectotype: BMNH 1871. 9.13.128, 82 mm SL, Mr. Schmeltz, Port Bowen, Queensland.

Paralectotype: BMNH 1871, 9.13.127, 72 mm SL, Port Mackay, Queensland.

Non-Type Specimens: Queensland — Endeavour River estuary, Cooktown, AMS I. 1488-90 (3); Finches Bay, Cooktown, AMS I. 14515; Murray River, Hinchinbrook Passage, QM I. 16543, QM I. 16546; Cape Cleveland, QM I. 5626; Townsville, QM I. 12233; Cape Bowling Green, QM I. 1966, QM I. 1968; Burdekin River, AMS I. 18330-1 (2), AMS I. 18333; Mackay, NMNZ P. 10166 (5); Yeppoon, QM I. 11625, QM I. 11637; Keppel Sands, AMS IA. 7700; Mackenzie I., Fitzroy River, AMS IB. 1259-60 (2); Wide Bay, AMS I. 9501-2 (2); Sandgate, QM I. 333; Logan River, QM I. 10889 (2); Redland Bay, QM I. 8054; Moreton Bay, N. of N.E. corner of St. Helena I., QM I. 10099; Pelican Banks, AMS I. 19565-001 (2+1 skeletonized), no further data, AMS I. 7734, AMS I. 12556, QM I. 334, QM I. 13103, WAM P. 25737-009.

New South Wales — Iluka, AMS I. 18061-005 (5); Smith's Lake, NMNZ P. 10165; Australia — ANSP 121574.

Marilyna meraukensis (de Beaufort, 1955)

(Figs. 2A, B; 5B; 6A)

Tetrodon staigeri (not of Castelnau). Webber, 1908, 209, 212, 216, 264; de Beaufort, 1955, 53.

Sphoeroides meraukensis. de Beaufort, 1955, 53-54.

Torquigener meraukensis. Munro, 1956, 294.

Takifugu meraukensis. Munro, 1967, 549; Allen, 1975, 95.

DIAGNOSIS

Marilyna with spines covering body from posterior of nasal organs to about mid-way between pectoral and dorsal fins; dorsal colour pattern consists of small irregular, dark spots, lessening in intensity in adults, dorsal bands lacking. Upper and lower lateral lines meet on caudal peduncle.

Prefrontals anterolaterally pointed, posterolaterally rounded, with extensive foramina; sphenotic wings extend anterolaterally over orbit in close contact with frontals; small triturating teeth present on upper jaw.

DESCRIPTION

The following meristic counts and proportions are for the lectotype (196 mm SL), and, in parenthesis, the range for 8 paralectotypes (16-158 mm SL) and 13 non-type specimens (73-161 mm SL).

Dorsal rays 11 (10-11); anal rays 9 (9-11); pectoral rays 19 (17-20); caudal rays 11 (11); vertebrae (8 + 9, 8 + 10).

Body robust, broadly rounded dorsally and flattened ventrally, elongate, tapering to a deep caudal peduncle. Head length 3.4 (2.9-3.3) in SL; snout to anterior of vent 1.6 (1.4-1.6) in SL, to origin of dorsal fin 1.5 (1.4-1.5) in SL, to origin of anal fin 1.4 (1.3-1.5) in SL, to origin of pectoral fin 2.9 (2.6-2.8) in SL; body width at base of pectoral fin 3.6 (2.7-3.4) in SL; depth from dorsal fin origin to anal fin origin 4.1 (3.8-4.3) in SL; body depth at posterior end of dorsal fin base 5.8 (5.4-6.4) in SL; least depth of caudal peduncle 8.5 (7.5-9.1) in SL.

Mouth small and terminal on a short snout, width 1.8 (2.2-2.7) in HL; lips thick, covered with numerous short papillae. Chin lacking. Nasal organ a short flattened papilla, posteriorly just level with eye, with 2 widely separated openings, the posterior one larger; inner surface of papilla with a large fold sited posteriorly on medial portion and about 4 smaller folds sited posteriorly on the ventral portion. Snout to anterior edge of nasal organ 2.2 (2.9-3.6) in HL; posterior edge of nasal organ to anterior edge of eye 6.4 (6.1-7.0) in HL.

Eye round, moderate in size and rim completely adnate, with the upper border just below dorsal profile, and the lower border just above level of mouth corner; horizontal diameter 5.3 (4.3-5.4) in HL. Anterior edge of gill opening smooth. Posterior of eye to dorsal corner of gill opening 1.5 (1.7-2.0) in HL.

Pectoral fin margins rounded; 1st ray very short; maximum length of fin from base 5.9 (5.4-6.7) in SL; top of fin base well above lower margin of eye. Dorsal fin located posterior to vent, fails to meet caudal fin base, distal margin bluntly pointed; 1st ray 10.9 (10.3-18.4) in SL; longest ray 5.8 (5.1-6.4) in SL; base length 8.9 (8.6-10.7) in SL and 1.5 (1.4-1.8) in longest ray. Anal fin base below posterior half of dorsal fin base, distal margin bluntly pointed and fails to reach caudal fin base; 1st ray 11.5 (11.1-20.1) in SL; longest ray 5.6 (5.4-6.4) in SL; base length 12.3 (10.6-14.0) in SL and 2.2 (1.9-2.3) in longest ray. Caudal fin truncate, maximum length 4.5 (3.8-4.9) in SL.

Ventrolateral skin fold extending from behind pectoral fin to caudal fin. Lateral line fairly distinct, encircling eye with a pre-opercular branch dropping to anterolateral limit of belly, running dorsolaterally along body towards caudal fin, rising over pectoral fin and gently dropping under dorsal fin to the lower one-third of the caudal peduncle, before rising to the middle of the caudal fin base; dorsolateral branches of lateral line above pectoral fin base not meeting

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in midline; anterodorsal branch anterior to nasal papillae almost meeting in midline; second lateral line dropping from behind mouth corner, extending along lateral region of belly and curving almost to pectoral fin base, continuing along belly from posterior limit of belly spines, crossing over ventrolateral skinfold to meet upper lateral line about half-way along caudal peduncle. Body spines multi-rooted, all short and surrounding body from behind nasal organs to about mid-way between pectoral and dorsal fins.

Colour in alcohol: base colour pale or greyish-brown, usually with dense dorsal covering of small, irregular brown spots. These are especially distinctive in younger specimens but tend to lessen in intensity in larger forms (see de Beaufort, 1955), although still discernable in the largest specimen examined here (SL = 161 mm). Dark patch at base of pectoral fin, otherwise fins and belly pale.

DISTRIBUTION

It is recorded from north-west Western Australia to the Gulf of Carpentaria and also from Merauke River, West Irian.

REMARKS

Superficially more similar to *M. darwinii* than to its other congener, *M. meraukensis* is the only *Marilyna* species that apparently lacks any form of banded colour pattern.

The meeting of upper and lower lateral lines on the caudal peduncle is only considered to be of specific significance, despite the higher level of significance usually accorded to lateral line pattern (for example, by Fraser-Brunner, 1943).

Although *M. meraukensis* is now known from an extensive northern Australian coastline, it has only previously been recorded from Western Australia, in the Prince Regent River (Allen, 1975).

De Beaufort (1955), although noting the total length of the largest of his examples of *meraukensis*, did not specify a holotype. However, the largest (ZMA 104.139), in the Type Catalogue of the Zoological Museum (currently in press, Dr. H. Nijssen, pers. comm.), is nominated as lectotype. Only 5 specimens apparently remain from the original series of 6 collected by Koch (see Weber, 1908, de Beaufort, 1955).

SPECIMENS EXAMINED

(n = 25; 2 or more specimens in a lot indicated by number in parenthesis).

Lectotype: ZMA 104.139, 196 mm SL, Batavian Marine Research Laboratory Coll., Dec. 1937, Merauke R., West Irian.

Paralectotypes: ZMA 104.140 (3), 65-86 mm SL, data as for lectotype; ZMA 104.141 (5), 16-158 mm SL, Dr Koch, 1904, Merauke R., West Irian.

Non-type specimens: Western Australia — Prince Regent River, Kimberley District, WAM P. 25038-003; Kalumbaru Mission, WAM P. 13485; Forest River Mission, AMS IB. 2835, 2837-8 (3); Medusa Bank, WAM unnumbered:

Northern Territory — Mickett Ck., Shoal Bay, NTFD unnumbered; Cape Condor, Melville Island, AMS IA. 7817; Darwin, NMNH B. 1476 (1 of 2 specimens):

Queensland — Gulf of Carpentaria, 17° 30.6'S 140° 32.6'E, CSIRO A. 2896, 17° 37'S 140° 13.8'E, CSIRO.C. 3408, no further data, CSIRO C. 3646; Norman River, QM I. 10851 (3 + 1 skeletonized).

Marilyna darwinii (Castelnau, 1873)

(Figs. 3A, B; 5C)

Tetrodon darwinii Castelnau, 1873, 94; MacLeay, 1881, 277; ———, 1882, 341.

Tetraodon darwini. Le Danois, 1961, 473.

Tetrodon fasciatus (not of Bloch & Schneider; not of McClelland) MacLeay, 1878, 365, 367, Pl. 10; ———, 1881, 276; ———, 1882, 340; Regan, 1903, 302; Fowler, 1928, 471; de Beaufort, 1962, 383.

Tetrodon pleurostictus. Regan, 1903, 302 (part); Weber, 1908, 209, 212, 216, 264; de Beaufort, 1962, 383.

Sphoeroides pleurostictus. Fowler, 1928, 468 (part); de Beaufort, 1962, 376, 382-3 (part); Taylor, 1964, 297; Roberts, 1978, 70.

Sphoeroides pleurostictus. McCulloch, 1929-30, 431 (part); Marshall, 1964, 493-4, colour pl. 70 (part); ———, 1966, 221, colour pl. 70 (part).

Torquigener pleurostictus. Fraser-Brunner, 1943, 11 (part); Munro, 1956, 294.

Colomesus fasciatus (not of Bloch & Schneider). Le Danois, 1959, 211, 246, 253, 255 (part); Tyler, 1964, 127 (part).

Gastrophysus pleurostictus. Whitley, 1965, 59 (part); Carcasson, 1977, 275 (part).

Torafugu pleurostictus. Munro, 1967, 549.

Tetraodon fasciatus. Stanbury, 1969, 210.

DIAGNOSIS

Marilyna with spines restricted to dense patches on dorsum, extending from level with nasal organs to posterior of pectoral fin; and on belly, distributed from level with posterior margin of eyes almost to vent; occasionally a few spines scattered on sides anterior to pectoral fin. Three broad, dark coloured bands cross dorsum, but usually absent from caudal penduncle.

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Prefrontals somewhat rectangular in outline, with very extensive olfactory nerve foramina. Sphenotic wings extend anterolaterally over orbit, well clear of frontals. Distinct triturating teeth lacking from upper jaw.

DESCRIPTION

The following meristic counts and proportions are for 25 non-type specimens (53-148 mm SL).

Dorsal rays 10-11; anal rays 8-9; pectoral rays 17-19; caudal rays 11; vertebrae 8 + 11, 9 + 11.

Body robust, broadly rounded dorsally and flattened ventrally, elongate, tapering to a deep caudal peduncle. Head length 2.7-3.3 in SL; snout to anterior of vent 1.5-1.6 in SL, to origin of dorsal fin 1.4-1.5 in SL, to origin of anal fin 1.4-1.5 in SL, to origin of pectoral fin 2.6-2.8 in SL; width of body at base of pectoral fin 2.8-3.2 in SL; depth from dorsal fin origin to anal fin origin 3.8-4.4 in SL; body depth at posterior end of dorsal fin base 5.2-6.0 in SL; caudal peduncle length 4.0-4.7 in SL; least depth of caudal peduncle 7.5-8.8 in SL.

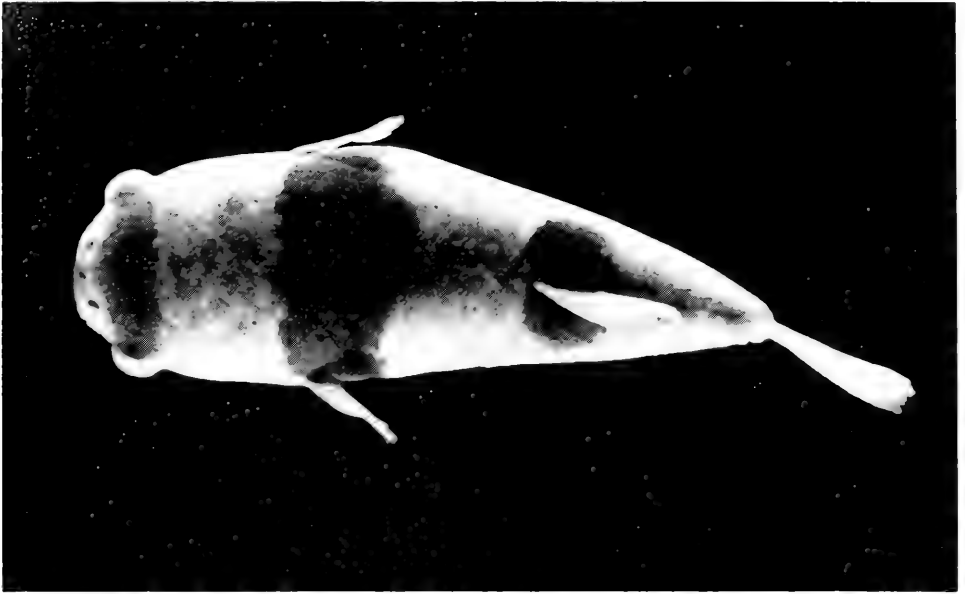
Mouth small and terminal on a short snout; width 2.5-3.5 in HL. Lips thick, covered with numerous short papillae. Chin lacking. Nasal organ a short, flattened papilla, posteriorly just level with eye, with 2 widely separated openings, the posterior one largest; inner surface of papilla with a large fold sited posteriorly on medial portion and 3-9 smaller folds sited posteriorly on the ventral portion. Snout to anterior edge of nasal organ 2.9-3.9 in HL; posterior edge of nasal organ to anterior edge of eye 6.7-9.5 in HL.

Eye round, moderate in size, and rim completely adnate with the upper border just below dorsal profile, and the lower border just above level of mouth corner; horizontal diameter 3.8-4.9 in HL. Anterior edge of gill opening smooth. Posterior of eye to dorsal corner of gill opening 1.9-2.1 in HL.

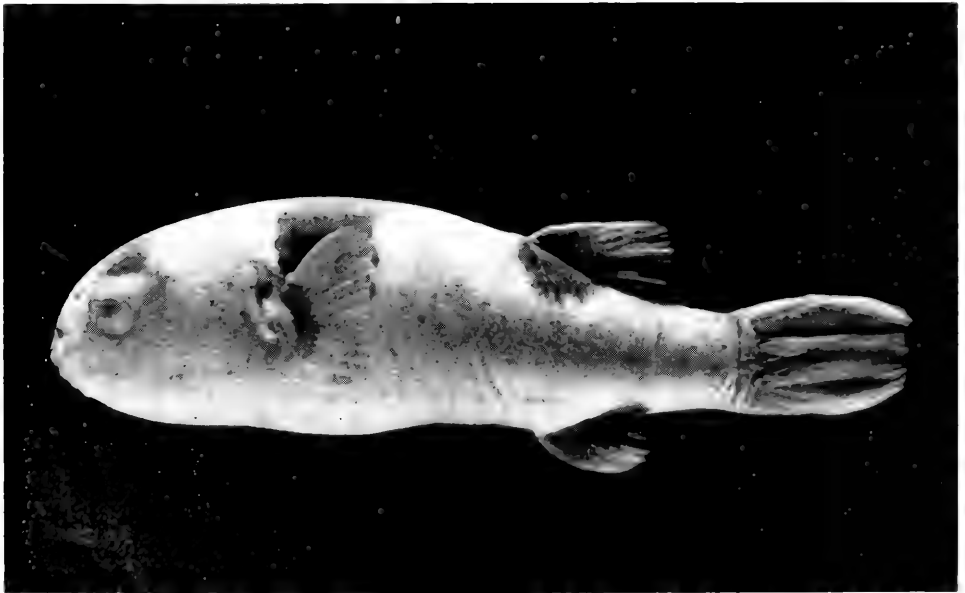
Pectoral fin margins rounded; 1st ray very short; maximum length of fin from base 5.6-6.9 in SL; top of fin base above lower margin of eye. Dorsal fin located posterior to vent, fails to meet caudal fin base, distal margin bluntly pointed; 1st ray 7.0-15.4 in SL; longest ray 5.0-6.2 in SL; base length 9.0-10.7 in SL and 1.5-2.0 in longest ray. Anal fin base below posterior half of dorsal fin base, distal margin bluntly pointed and fails to reach caudal fin base; 1st ray 9.0-15.3 in SL; longest ray 5.3-6.1 in SL; base length 12.1-15.8 in SL and 2.0-2.8 in longest ray. Caudal fin truncate; maximum length 3.4-4.2 in SL.

Ventrolateral skin fold extending from behind pectoral fin to caudal fin. Lateral line fairly distinct, encircling eye with a pre-opercular branch dropping to anterolateral limit of belly, running dorsolaterally along body towards caudal fin, rising over pectoral fin and sharply dropping under dorsal fin almost to ventrolateral skinfold, before rising to the middle of the caudal fin base; dorsolateral branches of lateral line above pectoral fin base not meeting in midline; antero-

Fig. 3. *Marilyna darwinii* NMNZ P. 10167, 127 mm SL.



A. Dorsal view.



B. Lateral view.

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dorsal branch anterior to nasal papillae almost meeting in midline; second lateral line dropping from behind mouth corner, extending along lateral region of belly and curving almost to pectoral fin base, continuing along belly from posterior limit of belly spines, medial to ventrolateral skin fold, almost to caudal fin. Body spines multi-rooted, all short and usually restricted to two dense arrangements, one mid dorsally in a rounded patch from nasal organs to posterior margin of pectoral fins, and the other mid ventrally in a larger patch extending from posterior margin of eyes almost to vent; occasionally a few spines on sides anterior to pectoral fin.

Colour in life (based on underwater observations): dorsum greenish-yellow with grey mottling; 3 broad, dark bands cross dorsum between eyes at mid-dorsum and at dorsal fin base; sides with a yellow-silverish sheen; belly and chin white; all fins bright yellow.

Munro (1967) recorded a dark bar also on the posterior end of the caudal peduncle, in examples, which he called *Torafugu pleurostictus*, from New Guinea.

DISTRIBUTION

It is recorded from the extreme north-east coast of Cape York Peninsula, N. Queensland, and extending along the northern Australian coastline to Cape Lambert, N.W. Western Australia, and also from Daru, Papua New Guinea.

REMARKS

This species was first described from Port Darwin, N.T., by Castelnau (1873) (as *Tetrodon darwinii*). Although much of the description is non-specific, the following characteristics were described; broad back, in part spiny; prominent nasal organs; obtuse snout; no trace of spots. The colour (based on a preserved specimen) was suggested as yellow, with the upper parts slaty blue, and with yellow fins. The yellow may be an artifact. Significant however is the absence of spots in a "three and a half inch" specimen, which is most suggestive that the congener, *M. meraukensis*, was not the species being described. Consequently, I am of the opinion that Castelnau's specimen was of the species later described by MacLeay (1878) as *Tetrodon fasciatus*, and still later, included in the synonymy of *T. pleurostictus* Günther by Regan (1903).

The name *darwinii* has received little acknowledgement from ichthyologists, and MacLeay (1878, 1881, 1882) completely overlooked the significant points made in Castelnau's description, whilst describing and later listing *fasciatus* in his various catalogues of Australian fishes. Regan's (1903) synonymisation of the species (which he referred to as *T. fasciatus*) with *pleurostictus*, did not take into account the significant differences of spination in the two species, an aspect noted but not resolved by de Beaufort (1962). The only reference to *T. darwinii* this century was in the synonymy of *Colomesus fasciatus* given by Le Danois (1959), an unfortunate grouping of species under the latter name, and in that author's (1961) catalogue of types in the Paris Museum. In the type

catalogue, three examples are listed (as Holotype!), but my reading of Castelnau's description strongly suggests that only a single specimen was described. My examination of the Paris Museum specimens shows NMNH B. 1475 to be *darwinii* and B. 1476 (2 spms) to be *darwinii* and *meraukensis*. The degree of shrinkage undergone by the largest specimen (B. 1475) is unknown; however the specimen would now seem to be rather too small when compared with Castelnau's measurement of three and a half inches. The type status thus remains unresolved.

MATERIAL EXAMINED

(n = 47; 2 or more specimens in a lot indicated by number in parenthesis).

Western Australia — Derby, SAM F. 92; W. of Cape Lambert, WAM P. 7611; Northern Territory — Cape Conder, Melville I., AMS IA. 7815-6 (2); Darwin, AMS I. 16426-001 (11) (Types of *T. fasciatus* MacLeay), NMNH B. 1475, 1476, (1 of 2 spms); Nightcliffe, USNM 173983:

Queensland — Escape River estuary, Cape York Peninsula, AMS I. 20929-009 (2), QM I. 15859; Weipa, NMV A. 560; Gulf of Carpentaria, Norman R., AMS I. 15552-021 (3 + 1 skeletonized), CSIRO A. 3655; Karumba Point, NMNZ P. 10167 (4); Karumba, AMS unreg., 17° 37.0'S 140° 13.8'E, 2m, CSIRO C. 3407:

Papua New Guinea — Daru, USNM unreg. (10). No data — SAM F. 2159 (4).

KEY TO *Marilyna* SPECIES

- | | |
|--|---------------------|
| 1. Dorsum completely devoid of spines | <i>pleurosticta</i> |
| Dorsum with spines | 2 |
| 2. Spines very sparse or absent from lateral surface of body; three dark bands across dorsum | <i>darwinii</i> |
| Spines dense on lateral surface of body; dorsum may be spotted, but never with bands | <i>meraukensis</i> |

Reicheltia n. gen.

Type species: *Sphaeroides halsteadi* Whitley, 1957, 70, fig. 12.

DIAGNOSIS

Same for *R. halsteadi* (Whitley)

ETYMOLOGY

The genus is named for John and Bonnie Reichelt, friends who assisted in seine netting along the southern New South Wales coast, whereby new locality records for *R. halsteadi* were obtained.

REMARKS

Reicheltia is a monotypic genus established for *Sphaeroides halsteadi* Whitley, previously recognised only from Sydney Harbour. Although possessing a completely adnate eye and ventrolateral skin fold, characteristics common also to *Marilyna*, *Reicheltia* differs from the latter, in having a less robust, dorsally flattened body form, with the eye level with or slightly interrupting the dorsal profile. In addition, the different structure of neural spines on the caudal peduncle of *Reicheltia halsteadi* results in it having a significantly smaller 'least caudal peduncle depth' than similarly sized *Marilyna* specimens (see fig. 6). Because of the rather generalised structure of the axial skeleton in *Torquigener* and related genera, little has been forthcoming by way of generic characteristics from this structure. In this instance, however, the relatively short and broad neural spines of *Reicheltia* serve to distinguish the genus from *Marilyna*.

Reicheltia halsteadi (Whitley, 1957)

(Figs. 4A, B, C; 5D; 6B)

Amblyrhynchotus oblongus (not of Bloch). Waite, 1900, 207 (part); Allen *et al.*, 1976, 441 (part).

Sphaeroides oblongus (not of Bloch). Waite, 1904a, 218.

Sphaeroides oblongus (not of Bloch). Waite, 1904b, 57.

Sphaeroides halsteadi Whitley, 1957, 70, Fig. 12; ———, 1965, 59.

DIAGNOSIS

A species, representing a monotypic genus of tetraodontid fishes, with the following combination of characters; nasal organ with two small, almost equally sized openings; eye rim completely adnate; top of pectoral fin base below lower margin of eye, ventrolateral skin fold present; shallow caudal peduncle (least depth $> 9.5 \times$ in SL); prefrontals moderately large, rounded, each with a small olfactory nerve foramen; frontals wide over orbit; sphenotic not contacting supraoccipital; triturating teeth absent; spines restricted to nape and belly.

DESCRIPTION

The following meristic counts and proportions are for the holotype (97 mm SL) and, in parenthesis, the range for 28 non-type specimens (24-120 mm SL).

Dorsal rays 10 (9-11); anal rays 7 (7-8); pectoral rays 16-17 (15-18); caudal rays 11 (11); vertebrae 8 + 10 (7 + 10, 8 + 10, 8 + 11, 9 + 10).

Body elongate, rounded dorsally and somewhat flattened ventrally, tapering to a narrow caudal peduncle. Head length 3.2 (2.7-3.3) in SL; snout to anterior of vent 1.5 (1.5-1.6) in SL, to origin of dorsal fin 1.5 (1.4-1.5) in SL, to origin



Fig. 4a. *Reicheltia halsteadii*
Holotype, AMS IB. 3623, 97 mm SL.

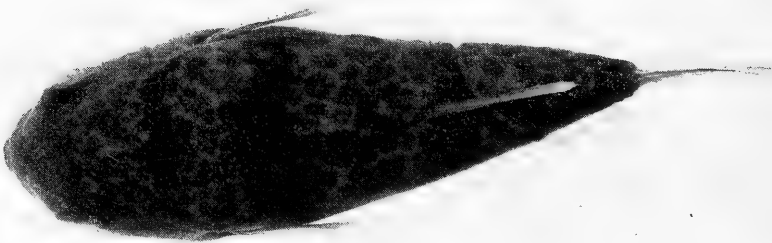


Fig. 4b. *Reicheltia halsteadii*
AMS I. 17759-002, 67 mm SL, dorsal view.

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of anal fin 1.4 (1.3-1.4) in SL, to origin of pectoral fin 3.0 (2.5-3.0) in SL; body width at base of pectoral fin (distorted in holotype) (2.9-3.8) in SL; depth from dorsal fin origin to anal fin origin 3.8 (3.8-4.5) in SL; depth of body at posterior of dorsal fin 5.2 (5.2-6.6) in SL; caudal peduncle length 4.7 (4.2-4.8) in SL; least depth of caudal peduncle 11.7 (9.9-11.9) in SL.

Mouth small, terminal, width 3.2 (2.7-3.6) in HL. Lips moderately thick, covered with numerous short papillae. Chin lacking. Nasal organ a short, flattened papilla, anterior to eye, with 2 widely separated openings, posterior opening slightly larger; inner surface of papilla with several well developed flaps around circumference. Snout to anterior edge of nasal organ 2.9 (2.5-3.5) in HL; posterior edge of nasal organ to anterior edge of eye 8.4 (5.4-8.5) in HL.

Eye round, moderate in size, and rim completely adnate, with the upper border level with or slightly interrupting dorsal profile, and the lower border well above level of mouth corner; horizontal diameter 3.8 (2.9-3.9) in HL. Anterior edge of gill opening smooth. Posterior of eye to dorsal corner of gill opening 2.4 (2.1-2.7) in HL.

Pectoral fin margins rounded; 1st ray very short; maximum length of fin from base (fin damaged in holotype) (4.6-6.2) in SL; top of fin base just below lower margin of eye. Dorsal fin located about level with vent, fails to meet

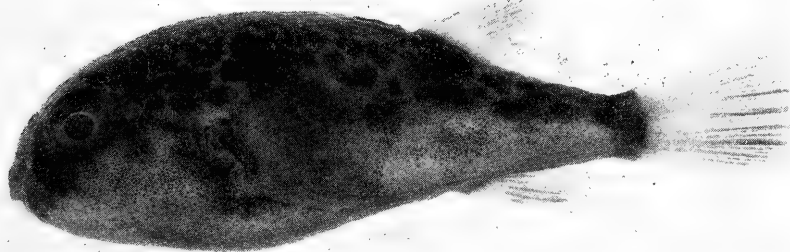


Fig. 4c. *Reicheltia halsteadii*

AMS I. 17759-002, 67 mm SL, lateral view.

caudal fin base, distal margin rounded; 1st ray 26.9 (8.0-27.6) in SL; longest ray 6.3 (4.8-6.3) in SL; base length 9.8 (8.9-11.4) in SL and 1.6 (1.5-1.9) in longest ray. Anal fin base below posterior half of dorsal fin base, distal margin rounded and fails to reach caudal fin base; 1st ray 17.0 (8.9-24.3) in SL; longest ray (damaged in holotype) (5.3-7.5) in SL; base length 17.6 (14.1-19.0) in SL and 1.9 (1.9-3.1) in longest ray. Caudal fin rounded ventrally, otherwise truncate; maximum length 4.6 (3.4-4.6) in SL.

Ventrolateral skin fold extending from behind pectoral fin margin to caudal fin; lateral line with small associated papilla, the line distinct on head and dorsum, indistinct on caudal peduncle, encircling eye with an anterodorsal branch almost meeting mid-dorsally anterior to nasal organ and a pre-opercular branch extending almost to pectoral fin base; dorso-lateral branches of lateral line above pectoral fin base may meet in midline; second lateral line dropping from behind mouth corner, extending along lateral region of belly to pectoral fin base; body spines short, 2-rooted, densely scattered on dorsum from between eyes to midway between pectoral fin base and anterior end of dorsal fin base, and on belly from beneath eyes to about 2/3 distance between pectoral fin base and vent; lateral surface free of spines.

Colour in alcohol (holotype): dorsum to mid-lateral surface dark brown; slightly darker bands cross mid-dorsal region and at base of dorsal fin; lower lateral surface silvery with many very small darker flecks; belly uniformly pale.

Colour in life (based on underwater observations): ground colour of dorsum pale yellowish-green with many irregular light brown or reddish-brown blotches; darker brown bands cross dorsum at eyes, between eyes and pectoral fin base, just behind pectoral fin base and extending down side at dorsal fin base, and at caudal fin base; brownish blotches and yellowish-green background continue to mid-lateral region, thereafter replaced by small, silverish-grey flecks gradually merging into white belly, silverish-grey sheen obvious on cheek and lower lateral surfaces; silverish-grey flecks form dense band under mouth, and are scattered thinly anterior to vent on spineless region of belly, at posterior of anal fin base and on undersurface of caudal peduncle (intensity and number of flecks vary according to individual); spinose region of belly white; all fins pale, a reddish-brown patch on anterior of pectoral fin insert.

DISTRIBUTION

It is recorded from the Noosa River, southern Queensland, to Bermagui (R. H. Kuitert, pers. comm.), southern New South Wales and also from Lord Howe Island.

REMARKS

Previously *R. halsteadi* was one of the poorest known of the validly named Australian pufferfish species, and had been identified only from Sydney Harbour. However, referring to examples obtained by the "Thetis" Expedition (AMS I. 4060-2

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(3 spms)), Waite (1900) reported the species from Lord Howe Island, under the name *Amblyrhynchotus oblongus*.

Other (larger) specimens referred to *A. oblongus* by Waite (1900) were examples of *Torquigener pleurogramma*, and were recorded separately by Waite (1904a) as *Spheroides hypselogeneion*. The reference to *Sphaeroides oblongus* from New South Wales by Waite (1904b) is most likely also referable to *Reicheltia halsteadi*.

MATERIAL EXAMINED

(n = 78; 2 or more specimens in a lot indicated by number in parenthesis).
Holotype: AMS IB. 3623, 97 mm SL, G. P. Whitley, 18/8/56, Chinaman's Beach, Middle Harbour, Sydney, N.S.W.

Non-type specimens: Queensland — Noosa R., QM I. 13769; Point Lookout, AMS IB. 2825, 18 m, QM I. 10882 (8); Stradbroke I., AMS IA. 6921, QM I. 10876 (5):

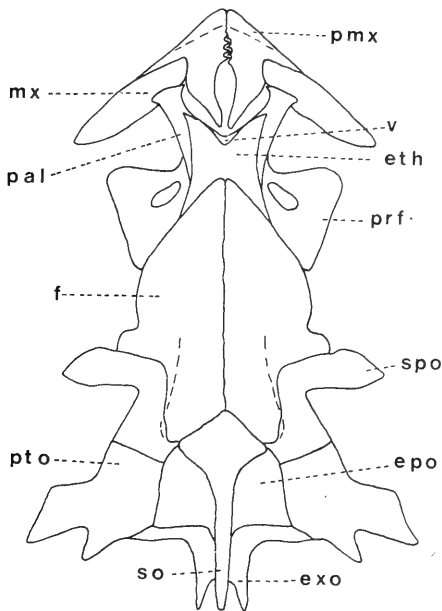
New South Wales — Ballina, 36 m, AMS IB. 6298, IB. 6299 (15); Yamba, 2 m, AMS I. 21687-002, NMNZ P. 10168 (skeletonized); Hawkesbury R., AMS I. 19938-002; Terrigal, AMS IB. 896 (3); Sydney Harbour, Chinaman's Beach, AMS IB. 3623, I. 19932-002 (7), I. 20325-001 (2), I. 20327-001 (2), I. 20335-005; Manly Cove, AMS I. 17760-005 (2), Bell's Head Bay, AMS I. 19934-002 (2); Middle Harbour, AMS I. 17023-001, I. 17759-002, Rose Bay, AMS I. 17927-002 (2), no further data, AMS I. 17215-002; Botany Bay, CSIRO C. 3710; Wattamolla Beach, 1 m, NMNZ P. 10169; Shoalhaven Bight, AMS IA. 7269-70 (2); Jervis Bay, AMS I. 21737-001 (7); Moruya, 1 m, AMS I. 21683-002 (3):

Lord Howe Island — AMS I. 4060-2 (3).

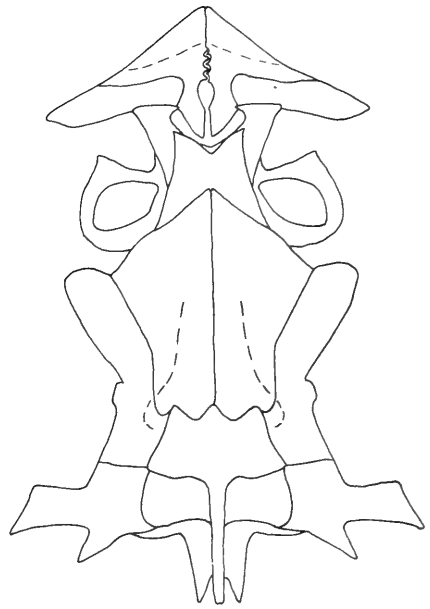
COMPARISON OF OSTEOLOGY OF *Marilyna* SPECIES AND *Reicheltia Halsteadi*

All three *Marilyna* species exhibit a larger than usual (in tetraodontids) olfactory nerve foramen in each prefrontal. Furthermore, the foramina progressively increase in size from *pleurosticta* to the largest in *darwinii* (see Figs. 5A, B, C). In *M. meraukensis* (particularly) and *M. darwinii* the large pre-frontals almost meet the anterolaterally extended sphenotics and, in the case of the former, largely exclude the frontals from the lateral edge of the orbit roof. Although the sphenotics are anterolaterally extended in *M. darwinii* as much as in *M. meraukensis*, the frontals in the former species are indented slightly over the orbit. The least specialised of the three species, *M. pleurosticta*, has the sphenotic wings shorter, and laterally produced, with correspondingly greater frontal contribution to the lateral orbit roof (see also Tyler, 1980, Fig. 267). In all three species, the frontals are reduced posteriorly, enabling contact to a greater or lesser degree of the sphenotic with the supraoccipital, a condition also characteristic of *Contusus* (Hardy, 1981b).

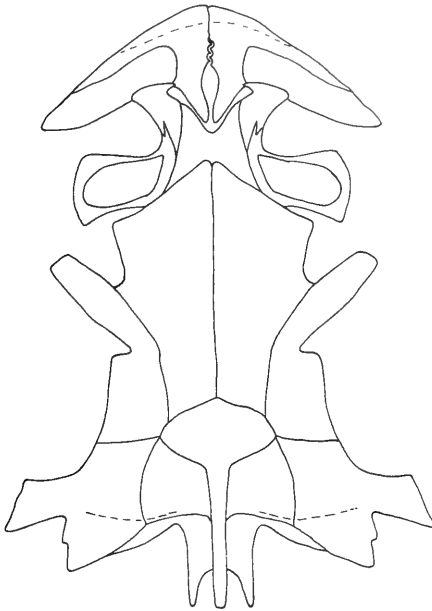
Fig. 5. Skull osteology of:



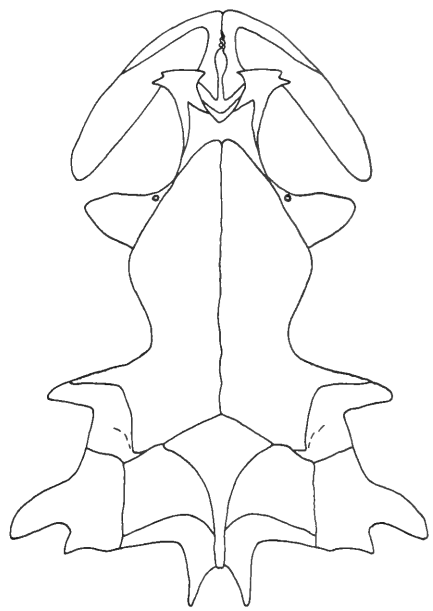
A. *Marilyna pleurosticta* (skull length 33 mm)



B. *M. meraukensis* (skull length 31 mm)



C. *M. darwinii* (skull length 43 mm)



D. *Reicheltia halsteadii* (skull length 41 mm)

Abb.: epo, epiotic; eth, ethmoid; exo, exoccipital; f, frontal; mx, maxillary; pal, palatine; pmx, premaxillary; prf, prefrontal; pto, pterotic; so, supraoccipital; spo, sphenotic; v, vomer.

Olfactory nerve foramina in the prefrontals of *R. halsteadii* are very much smaller than in *Marilyna* species and frontal contribution to the lateral edge of the orbit roof very much greater, owing to the smaller prefrontals and sphenotics (see Fig. 5D). The frontals widen over the orbit, reaching a maximum just posterior to their contact with the prefrontals, and are sufficiently wide posteriorly to exclude contact of the sphenotics with the supraoccipital. In addition, the frontals are extended anteriorly over a greater part of the ethmoid in *R. halsteadii* than in *Marilyna*. Of the 4 species, only *R. halsteadii* has the prefrontals failing to contact the palatines.

In both genera, the parasphenoid extends dorsally to the frontal, but with the septum incomplete, and prootic medial prongs absent. Triturating teeth are absent from *R. halsteadii* and *M. darwinii* but present though small, on the upper jaw in *M. pleurosticta* and *M. meraukensis*.

An interhyal is absent and dorsal hypohyal present in all species, with the branchial skeleton being similar throughout. The first pharyngobranchial is relatively narrow and curved, bearing many minute teeth, while the second and third pharyngobranchials have about 12 (16 in the second element in *R. halsteadii*) bulbous teeth; all species have a single row and three double rows of poorly developed gill rakers.

The axial and caudal skeletons are similar in most respects, being essentially typical of tetraodontids (see Tyler, 1964, 1980). In the four species, complete haemal arches are present on the 4 or 5 posteriormost abdominal vertebrae, and a small supraneural is present. Dorsal fin basal pterygiophores number 10 and anal fin basal pterygiophores number 6 (5 in *meraukensis* and *pleurosticta*). A significant difference between *Marilyna* and *Reicheltia* exists however, in the shape and height of the caudal vertebrae neural spines posterior to the dorsal pterygiophores

Fig. 6. Posteriormost caudal vertebrae and caudal skeleton:

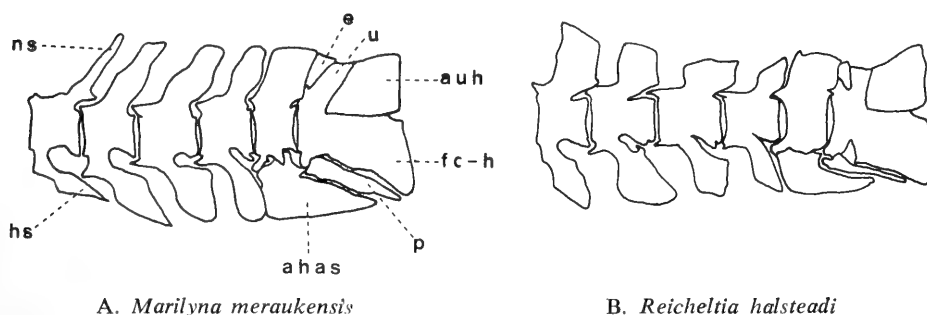


Abb.: ahas, autogenous haemal arch and spine; auh, autogenous upper hypural plate; e, epural; fc-h, fused centrum-lower hypural plate; hs, haemal spine; ns, neural spine; p, parhypural; u, urostyle process.

(see Fig. 6A, B). Those of *Marilyna* species are consistently narrower and longer than the corresponding elements in *Reicheltia*, resulting in the deeper caudal peduncle in the former. A well developed urostylar process is present in both genera.

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I am grateful to the curators of ichthyology at the institutions listed under Methods and Abbreviations, for the loan of material in their care. Mr. I. S. R. Munro kindly made available X-Ray facilities at CSIRO's Fisheries and Oceanography Division, Cronulla, and my wife continually helped in both encouragement and bibliographic research. Colleagues at the National Museum of New Zealand commented on the manuscript.

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A further description of the Musky Rat-Kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876 (Marsupialia, Potoroidae), with notes on its biology

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ABSTRACT

The Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, is described. Its present distribution and habitat are defined. An account is given of its diet and of its feeding, grooming, locomotory, nest-building, courtship and social behaviour. Earlier reports that two young may be reared simultaneously are confirmed. Attention is drawn to a number of unspecialised characters including the distribution of vibrissae, limb proportions, structure of the manus and pes, presence of a mobile hallux, the non-saltatory gait, presence of a vestigial lower second molar, and an unsacculated stomach. Although these characters indicate that *Hypsiprymnodon* is a 'primitive' macropod, it is concluded that there is such a close relationship between the Hypsiprymnodontinae and the Potoroinae that the subfamilial distinction is unwarranted, unless the macropods be elevated to a superfamily Macropodoidea, comprising the families Macropodidae and Potoroidae.

INTRODUCTION

Ramsay's (1876) description of the Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, included the dental formula, a brief description of the skull, a more detailed account of the external morphology, and brief notes on the biology. On the basis of two skins (including the skulls and the complete feet) sent to him by Ramsay, Owen (1877) erected a new genus and species, *Pleopus nudicaudatus*, but he later recognised the priority of Ramsay's taxon (Owen, 1878). Subsequently Owen (1879) provided a partial description with particular attention to the anatomy of the hind foot which, in his opinion, was so distinct as to warrant the erection of the family Pleopodidae to include this single species. Collett (1887), more correctly, erected the family Hypsiprymnodontidae to accommodate the genus. Thomas (1888), who made a brief diagnostic description of the genus and species based on his examination of a spirit specimen and on the published accounts of Ramsay and Owen, assigned *Hypsiprymnodon* to the sub-family Hypsiprymnodontinae within the family Macropodidae. Nine specimens

in North American collections, mostly skulls, were briefly commented upon by Tate (1948) who included the fossil *Propleopus oscillans* and the (then) fossil *Burramys parvus* within the sub-family.

Carlsson (1915) made a study of the anatomy of one adult and one pouch young, concentrating on the skeleton and muscles of the limbs. In an unpublished M.D. thesis, Heighway (1939) gave an account of the external characters of six specimens in the Department of Anatomy of the University of Sydney and of her dissection of one of these. Like Carlsson, she concentrated on the myology. Pearson (1950a, 1950b) described the reproductive tract of two female specimens. Working from three skulls, Ride (1961) made a more detailed study of the cheek-teeth. With twelve skulls at his disposal, Woods (1960) described the entire dentition and provided a succinct description of the skull itself. Of these authors, only Ramsay had observed living animals and had access to recently killed specimens.

In 1979 a captive colony of the Musky Rat-kangaroo was established at the Northern Regional Centre of the Queensland National Parks and Wildlife Service, Pallarenda, permitting more precise observations on the behaviour than hitherto possible (Fig. 1). Access to specimens taken in faunal surveys in north-eastern Queensland and those that have died in the captive colony has made possible a further description of the species.

MATERIALS AND RESULTS

FURTHER DESCRIPTION

The following is based on examination of 10 skins and 10 skulls from the Queensland National Parks and Wildlife Service (QNPS), the Queensland Museum (QM) and the Australian Museum (AM).

Study Skins:

N 30005 QNPS, Townsville
N 30007 QNPS, Townsville
N 30008 QNPS, Townsville
N 30010 QNPS, Townsville
J 145 QM, Brisbane
J 1823 QM, Brisbane
J 6818 QM, Brisbane
J 6822 QM, Brisbane
J 6826 QM, Brisbane
J 6829 QM, Brisbane

Skulls:

N 30001 QNPS, Townsville
N 30002 QNPS, Townsville
N 30003 QNPS, Townsville
N 30004 QNPS, Townsville
N 30005 QNPS, Townsville
N 30006 QNPS, Townsville
N 30007 QNPS, Townsville
N 30008 QNPS, Townsville
N 30009 QNPS, Townsville
A 9813 AM, Sydney

PELAGE

The fur on the back and sides is dense, soft to the touch, and a rich rufous brown ticked with dark brown. The basal two-thirds of most of the hairs of

the under-fur are a light blue-grey with the upper third a rich rufous brown; intermingled with these are similar hairs which are dark brown in the terminal third. Scattered dark brown guard hairs overlie the body hair. The fur of the head and face is short, soft and grizzled, the basal half of each hair of the under-fur being blue-grey and the terminal half pale grey with a short brown tip. These are intermingled with overlying dark brown guard hairs. The belly fur is less dense and of finer texture than the back fur and is light rufous brown in colour, the basal half of each hair being blue-grey and the terminal half light rufous brown: there are no guard hairs. Patches of white to cream fur are commonly present on the ventral surfaces of the throat and chest. The pelage of the back and sides is continued onto the legs but abruptly becomes very short about 15-20 mm above the ankles and wrists, giving the impression, as noted by Owen (1879), of 'the legs of a pair of trousers'. Fur extends for about 10 mm onto the base of the tail where it ends abruptly, the remainder of the tail being covered by a pavement of non-overlapping, rectangular to octagonal scales, brown on the dorsal surface of the tail, somewhat lighter below (Fig. 2). Occasional short hairs arise between the scales. The dorsal surfaces of the manus and pes are lightly furred with short, fine, dark brown hairs.

HEAD

The head is long and slender with no concavity in its profile. The rhinarium is hairless, dark brown in colour with a distinct median groove extending from the level of the nostrils to between the first upper incisors. Ventrally, the rhinarium



Fig. 1. Adult male *Hypsiprymnodon moschatus*, wild-caught near Innisfail, Queensland, and held in captivity at the Northern Regional Centre of the Queensland National Parks and Wildlife Service.



Fig. 2. Dorsal aspect of the tail of *Hypsiprymnodon moschatus*.

is expanded and confluent with the central part of the upper lip; dorsally it extends backwards, more than in species of *Potorous*, less than in species of *Bettongia*. The nostrils are somewhat more lateral in position than in these genera.

The ears are large and rounded with little tragal development and the external terminal half of the ear is covered in minute dark brown hairs. The prominent eyes have a dark brown iris and a round pupil. Small fine, dark brown eyelashes are present on the upper eyelid.

VIBRISSAE

Each side of the head bears 12-14 mystacial vibrissae arranged in three rows, 2 supraorbital vibrissae, 3 genal vibrissae and an indefinite number of submental vibrissae. On each forelimb are two long ulnar carpal vibrissae, a median antebrachial vibrissa and an anconeal vibrissa.

SHAPE AND SIZE

The body does not have the degree of disproportion between the fore and hindquarters typical of macropods.

According to Heighway (1939), the circumference of the body measured at the inguinal level is not more than 10% greater than at the level of the axillae. The tail is short and decreases in proportion to the length of the head

DESCRIPTION AND BIOLOGY OF *HYPSIPRYMNODON*

and body as animals grow. Data from Table I show that the tail is about 66% of the length of the head and body in animals of head and body length less than 250 mm; about 54% in the range 250-259 mm; and about 44% in the range 300-350 mm.

In the male, a posterior extension of the epididymes, separated from the other scrotal contents by a constriction, has the appearance of a secondary scrotum. The pouch of the female opens anteriorly and its opening is bordered by a dense fringe of long hairs. A narrow line of hair extends along the mid-dorsal surface of its lining. There are four nipples, each surrounded by a tuft of long pale brown hairs.

TABLE 1. Body dimensions (mm) and weight (g) of *Hypsiprymnodon moschatus*, partly from Heighway (1939). CA, circumference of body at axilla; CI, circumference of body at inguinal region; EH, ear height; EW, ear width; HB, length of head and body; HF, length of hindfoot; T, tail; W, weight.

	Sex	HB	T	CA	CI	EH	EW	HF	W
Heighway 4	?	341	137	206	231	29	22	60	—
Heighway 2	?	307	143	168	193	26	20	56	—
Heighway 3	F	303	143	181	200	26	20	59	—
Heighway 1	?	300	125	156	181	27	22	62	—
Heighway 6	M	292	150	181	206	24	19	61	—
Heighway 5	?	288	150	156	175	26	21	57	—
N30010	M	273	137	—	—	23	19	52	—
N30008	M	267	159	—	—	30	18	60	540
N30007	F	266	138	123	165	25	19	60	545
N30005	M	208	138	128	163	28	16	58	337
N30003	F	—	165	—	—	—	—	—	550
N30002	F	—	151	—	—	—	—	—	494
N30006	F	—	137	—	—	—	—	—	450
N30001	M	—	132	—	—	—	—	—	680
N30004	F	—	123	—	—	—	—	—	453
Mean		284	142	162	189	26	20	57	506
S.D.		34	11	45	22	2	2	3	100



Fig. 3. Right manus of *Hypsiprymnodon moschatus*.

MANUS

The manus (Fig. 3, Table 2) is heavily scaled dorsally and ventrally. The digits are radially disposed and sub-equal in length ($3 > 2 > 4 = 5 > 1$). Each digit bears a curved, sharp, but not markedly elongate claw, below which is a well-defined apical pad, the whorls of which have a predominantly longitudinal orientation.

There are four prominent, transversely striated interdigital pads, the pad between the first and second digits probably being fused with the thenar (inner metacarpal) pad. The hypothenar (outer metacarpal) pad is transversely striated and has a longitudinal median groove.

TABLE 2. Dimensions (in mm) of manus of *Hypsiprymnodon moschatus*. D_1 - D_5 , length of first to fifth digits. PL, palm length; PW, palm width.

	Sex	PL	PW	D_1	D_2	D_3	D_4	D_5
N30008	M	19.2	8.7	7.4	10.6	13.2	11.8	10.2
N30010	M	18.1	8.5	6.7	10.4	13.3	10.4	8.3
J6823	M	17.9	8.0	6.4	9.5	12.7	10.5	8.3
N30007	F	17.9	8.3	6.7	9.2	12.6	11.1	9.2
J145	M	17.7	7.9	7.2	10.4	12.7	10.0	8.8
J6822	M	17.0	8.3	7.0	9.3	12.7	11.8	9.8
J6826	M	16.6	8.7	6.7	9.2	11.8	10.8	9.5
J6829	F	16.5	8.3	6.7	10.6	12.7	10.3	8.7
N30005	M	16.0	7.7	6.2	8.9	10.9	9.5	8.2
Mean		17.4	8.3	6.8	9.8	12.5	10.8	9.0
S.D.		1.0	0.4	0.4	0.7	0.7	0.7	0.7



Fig. 4. Right pes of *Hypsiprymnodon moschatus*.

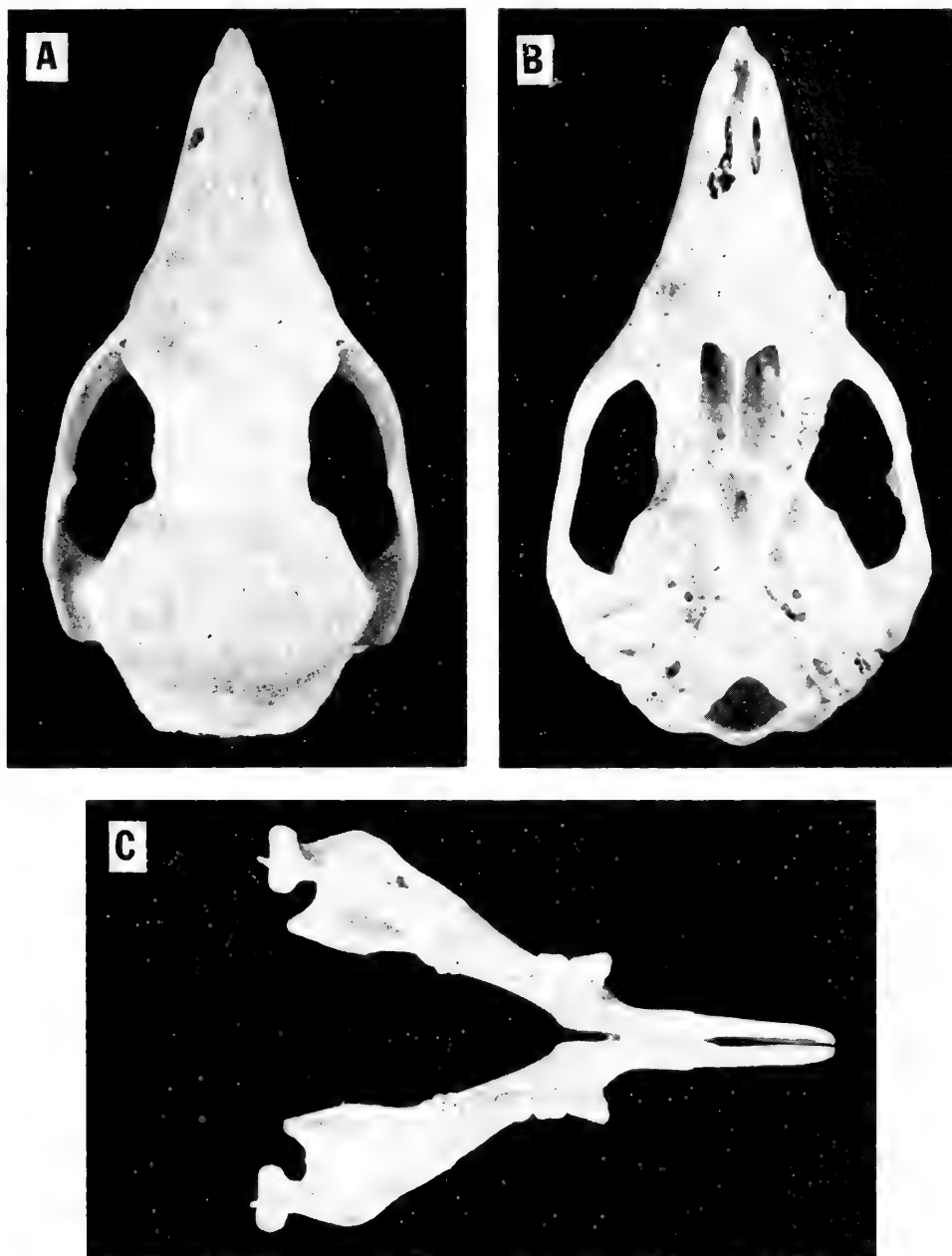


Fig. 5. A, dorsal aspect of skull; B, ventral aspect of skull; C, mandible of *Hypsiprymnodon moschatus* (QNPS N3003).

PES

The pes (Fig. 4, Table 3) is heavily scaled on the sole and the digits are completely covered by scales, interspersed on the dorsal and lateral surfaces with sparse, short hairs. The clawless first digit, which originates about halfway along the length of the foot, can be opposed almost to the outer edge of the sole. The second and third digits are syndactyl. The fourth digit, continuous with the axis of the foot, is the longest ($4 > 5 > 2 = 3 > 1$). The claws on the second to fourth digits are well developed, curved and sharp but not markedly elongate. All digits, including the syndactyl second and third, bear apical pads with whorls which are predominantly longitudinal in orientation. The four interdigital pads are transversely striated. The pad between the first and second digits is elongate and may represent a fusion with the thenar (inner metatarsal) pad. At the base of the syndactyl second and third digits is a U-shaped pad which obviously represents an interdigital pad between them. It is in partial contact with the pad between the syndactyl digits and the fourth digit. The pad between the fourth and fifth digits is elongate, as is the hypothenar (outer metatarsal) pad.

TABLE 3. Dimensions (in mm) of pes of *Hypsiprymnodon moschatus*. D_1 - D_5 length of first to fifth digits. SL, length of sole; SW, width of sole.

	Sex	SL	SW	D_1	D_{2-3}	D_4	D_5
N30007	F	39.0	10.3	14.2	12.0	21.4	18.0
N30008	M	38.9	11.2	13.5	12.6	23.9	17.7
J6826	M	38.6	10.7	14.0	12.4	20.6	15.8
J145	M	38.4	9.6	13.5	11.3	22.0	16.0
J6822	M	38.3	10.8	14.8	12.3	22.6	16.3
N30010	M	36.5	10.0	13.0	12.4	21.6	15.2
J6819	F	35.8	9.8	13.8	12.0	21.8	16.5
N30005	M	35.5	9.3	14.0	11.0	21.5	15.0
Mean		37.6	10.2	13.9	12.0	21.9	16.3
S.D.		1.5	0.7	0.5	0.6	1.0	1.1

SKULL

The following description draws attention to diagnostic differences between the skull of *Hypsiprymnodon moschatus* (Figs. 5, 6, Table 4) and those of *Potorous tridactylus* and *Bettongia lesueur* (Fig. 6).

The nasals, which are long and slender (broad in *Bettongia*), are in contact with the frontals at the level of the anterior border of the orbit (further forward in *Potorous*). The naso-maxillary suture is more than twice the length of the naso-premaxillary (slightly shorter in *Potorous*, sub-equal in *Bettongia*). The lacrimal barely extends beyond the rim of the orbit (contributes to the face in *Potorous*) and the lacrimal foramen lies just outside the rim (on, or slightly within, the rim, in *Potorous* and *Bettongia*). There are two infraorbital foramina (normally only one in other macropods) at a level anterior to the permanent premolar (level with the middle of the permanent premolar in *Potorous* and *Bettongia*). The zygomatic arch is slender as in *Potorous* (much less massive than in *Bettongia*). As in *Potorous*, but not in *Bettongia*, the zygomatic arch

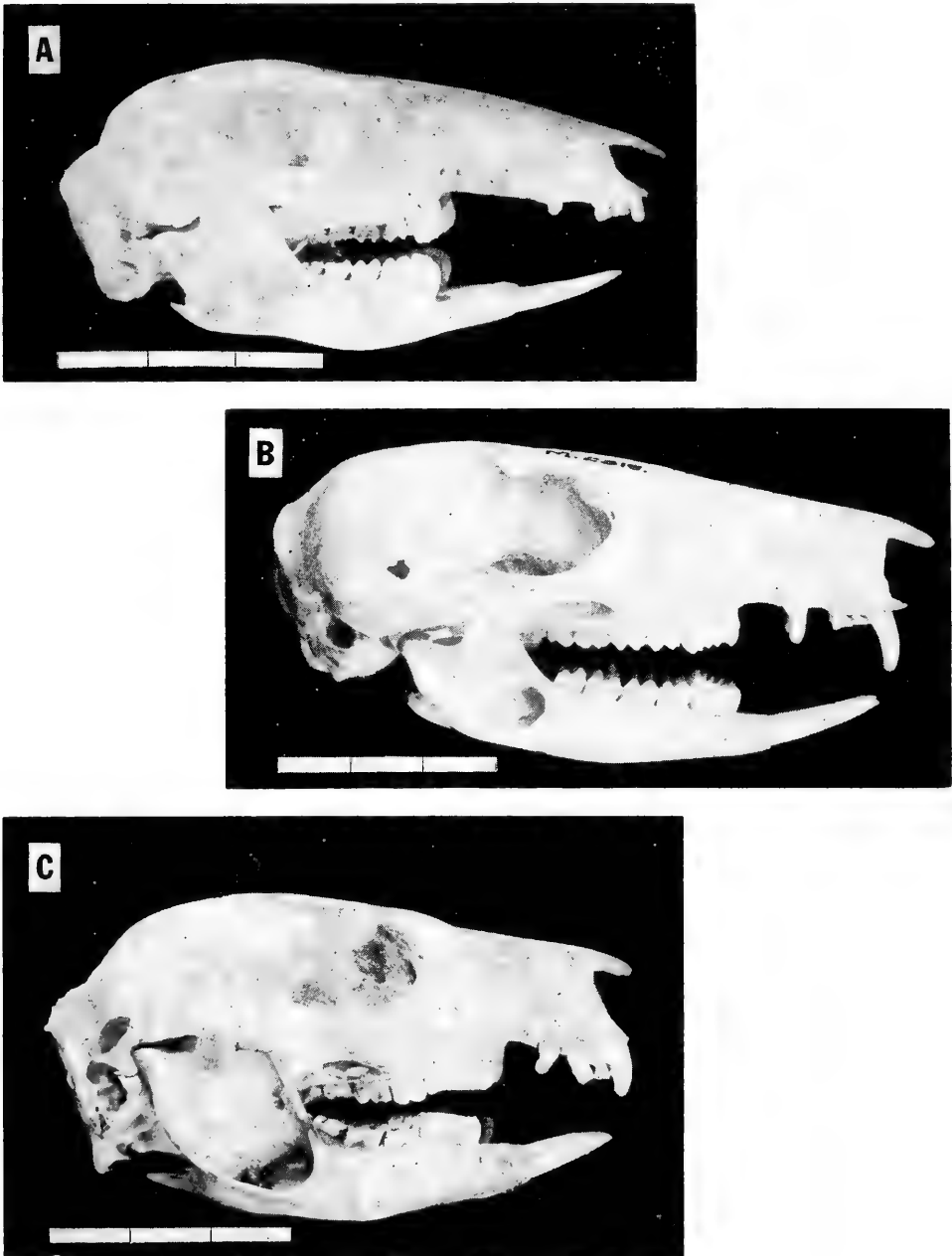


Fig. 6. Right aspects of skulls of A, *Hypsiprymnodon moschatus* (QNPS N30003); B, *Potorous tridactylus* (AM M2318); C, *Bettongia lesueur* (AM A9813). Scales in cm.

makes no contribution to an anterior suborbital shelf. Relative to the basicranial length, the length of the zygomatic arch is about the same as in *Potorous* (ca 55%) but much shorter than in *Bettongia* (ca 65%). The inferior anterior process of the zygomatic arch is much more weakly developed than in *Potorous*. There is a short contact between the frontal and squamosal (much longer in *Potorous* and usually so in *Bettongia*). There is no sagittal crest (weakly developed in *Potorous*) and the occipital crest is weakly developed (prominent in *Potorous* and *Bettongia*).

The anterior palatal vacuities are long, extending from the level of the third incisors to beyond the canines (not beyond the anterior border of the canines in *Potorous* and *Bettongia*). The posterior palatal vacuities are broad and long, extending posteriorly from the level of the first molar (from the level of the posterior edge of the third molar in *Potorous*) and bounded by slender processes of the palatines. The alisphenoid bullae are flat, as in *Potorous* (greatly inflated in *Bettongia*).

The mandible is arcuate ventrally, relatively shorter and stouter than in *Potorous*; longer and less massive than in *Bettongia*, reflecting the relatively greater length of the diastema. The distance between the base of the first lower incisor and permanent premolar is proportionately greater than in either *Potorous* or *Bettongia*. The height of the coronoid process relative to the length of the mandible (ca 50%) is greater than in *Potorous* (ca 40%) but much less than in *Bettongia* (ca 65%). The angular process is short and blunt as in *Potorous* (pointed in *Bettongia*). The angular inflection is markedly less developed than in *Potorous* and *Bettongia* and the masseteric fossa is somewhat more developed than in these. The condyle is only slightly above the level of the molar row (at about the same level as the molar row in *Potorous*, considerably higher in *Bettongia*).

TABLE 4. Dimensions (in mm) of skull of *Hypsiprymnodon moschatus*. BL, basicranial length; C-M₁, canine to fourth upper molar, inclusive; CH, height of condyle above base of dentary; CP, height of coronoid process above base of dentary; DL, length of dentary; IO, minimum interorbital width; M₁-M₄, first to fourth upper molars; NL, maximum length of nasal; NW, maximum width of nasal; ZW, maximum (zygomatic) width of skull.

	Sex	BL	ZW	C-M ₁	M ₁ -M ₄	IO	NL	NW	DL	CH	CP
A9813	M	—	35.0	27.1	10.9	12.0	29.5	4.1	36.6	9.9	17.6
N30009	F	54.8	32.6	25.8	11.7	11.0	29.1	4.0	34.7	9.0	16.8
N30003	F	54.2	34.1	25.2	11.4	11.1	29.7	4.5	34.5	9.9	18.4
N30001	M	54.1	33.6	25.6	10.8	10.6	29.3	4.8	34.2	10.0	18.6
N30007	F	54.1	33.6	25.7	11.0	10.8	30.1	4.3	34.8	10.7	17.3
N30002	F	52.9	32.9	24.8	11.1	10.7	—	4.9	34.1	9.7	17.1
N30008	M	49.9	31.0	24.4	11.3	10.9	27.2	3.8	31.5	8.2	15.5
N30006	F	49.1	31.7	23.9	10.8	10.9	26.3	3.7	31.7	9.5	17.6
N30005	M	48.1	30.7	22.4	10.3	10.8	22.0	3.8	31.3	8.8	—
N30004	F	47.7	30.5	23.2	11.6	10.4	—	3.7	30.8	8.3	15.7
Mean		51.7	32.6	24.8	11.1	10.9	27.9	4.2	33.4	9.4	17.1
S.D.		2.9	1.6	1.4	0.4	0.4	2.7	0.5	1.8	0.5	1.3

DENTITION

The detailed accounts of the dentition given by Woods (1960) and Ride (1961) make any further description or comment unnecessary but it should be noted that the second lower incisor is minute, nonfunctional and so directed that its anterior face is pressed against the surface of the mandible (Fig. 7). It was reported by Wood to be lost in the course of development but is present on either one or both rami of all adult mandibles examined in the course of this study. The second premolars, which are smaller than the third, coexist with these in young animals but are lost in the adults. The large sectorial third premolars are oriented obliquely.

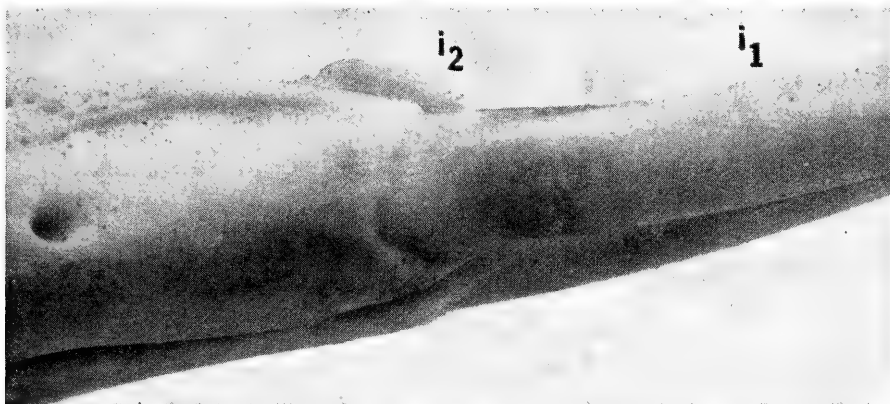


Fig. 7. Tip of dentary of adult *Hypsiprymnodon moschatus* (QNPS N3003) showing second lower incisor (i_2) overlapping base of first lower incisor (i_1).

DISTRIBUTION

Ramsay (1876) mentioned that the Musky Rat-kangaroo was 'by no means rare' in 'the dense brushes of the Rockingham Bay district' but found it difficult to collect due to its retiring habits and the nature of its habitat. The statement remains correct today, for it is still common throughout its range, although difficult to observe. The present distribution is from Ingham, north to Helenvale (35 km south of Cooktown) in tall closed forest at all altitudes (Fig. 8). It is most readily observed in moister areas, especially near to creeks and rivers, and in the northern part of its range it has been observed living near a spring in a small isolated block of tall closed forest.

BEHAVIOUR

The Musky Rat-kangaroo is diurnal and most readily observed in the early morning or late afternoon when it is moving about in search of food. Fruits of such trees as the King Palm (*Archonotophoenix alexandrae*), Kuranda Satin Ash (*Eugenia kuranda*), *Diploglotis* sp. and *Sarcotoechia* sp. are readily eaten. The

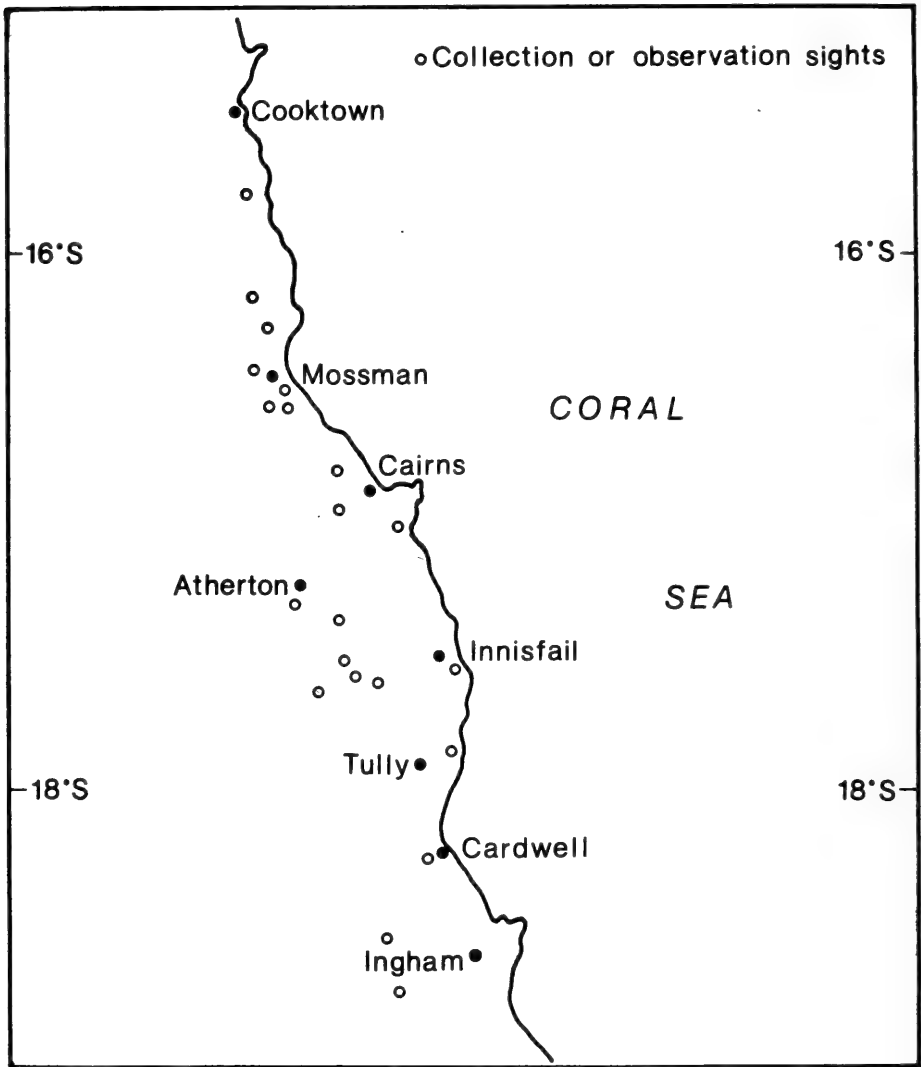


Fig. 8. Distribution of *Hypsiprymnodon moschatus*. Each open circle represents at least one capture or observation.

forepaws are used to turn over leaf litter in search of insect and vegetable food material. In captivity, grasshoppers and earthworms are readily eaten. Food material that is not too large to be lifted is picked up in the mouth and transferred to the forepaws to be held for consumption while the animal sits back on its hindfeet with the tail stretched out behind. When eating a grasshopper, the

Musky Rat-kangaroo holds the insect in its forepaws and turns its head to one side so that the sectorial premolars can shear through the chitinous exoskeleton. With the head then directed forward, the incisor teeth are used to pull the insect apart and, with the aid of the tongue, to take it into the mouth for thorough mastication.

Grooming behind the shoulder, on the flank, shoulder and neck, and in and around the ear is performed with the claws of the syndactylous toes of either hindfoot: other parts of the body are groomed with the claws of the forefeet or with the tongue.

The usual mode of locomotion is a slow gait in which the forepaws are placed on the ground and the hindfeet are brought forward in unison beneath the body. The tail does not act as a support, as in the slow gait of kangaroos, but is held stretched out behind the animal above the ground. Fast locomotion is a version of the slow gait and, unlike the fast gait of other macropods, is quadrupedal (Fig. 9). Adult Musky Rat-kangaroos have been observed to climb on fallen branches and horizontal trees and juveniles readily ascend a thin branch inclined at about 45° , but it has not yet been possible to determine the extent to which the hallux contributes to a grip of the hindfeet.



Fig. 9. Fast locomotion of *Hypsiprymnodon moschatus*. Outlines drawn from photographs of an individual in captivity at the Northern Regional Centre of the Queensland National Parks and Wildlife Service.

At night and in the middle of the day, the Musky Rat-kangaroo sleeps in a nest in a clump of lawyer vine or between the plank buttresses of large rain-forest trees. One nest, situated on the ground against such a buttress, was 60 cm long, 20 cm wide, and 8 cm high. It had no distinct form, appearing as an untidy pile of leaves, but at one end, at ground level, there was a round opening about 5 cm in diameter leading into an internal chamber lined with lichens and decayed fern fronds. Collett (1887) described the nests as round in shape but no nest fitting his description has been seen in the course of this study. As in potoroos and bettongs, nest material is picked up in the mouth, transferred to the forepaws, then placed on the ground in front of the hindfeet. The tail is curved down and forwards and, with the animal's weight taken on its forelimbs, the material is kicked into the curled tail by the hindfeet. The tail is tightened, grasping the material, and the animal moves off to the nest site carrying the small bundle behind it.

The Musky Rat-kangaroo appears to be solitary but aggregations of up to three individuals have been observed feeding on fallen rainforest fruit. Breeding occurs from February to July and is preceded by several days of courtship in which the male approaches the female face to face and both stand erect, touching each other's head and neck with their forepaws. Observations in the field and on captive animals confirm that two young are usually born and both may complete their development in the pouch. After about 21 weeks, the young leave the pouch and for several subsequent weeks spend a considerable part of the day in the nest. Older young accompany the mother while she is feeding, staying close at heel. Sexual maturity of females is reached at slightly more than a year of age.

DISCUSSION

Ramsay (1876) described the upper surface of the body as 'a rich golden colour, mixed with black' due to 'the base of the hairs being of a dull dark wood-brown, the remainder yellow and black barred'. Inasmuch as no mention is made of the uniformly coloured guard hairs, this description appears not to have been based on close observation but it is nevertheless surprising that the overall colour was described as 'golden'. Owen (1879) did not contradict Ramsay's description of colour but pointed out, correctly, that the body hair is 'of two kinds, the outwardly visible and longest being coarse and hard to the touch, that beneath forming a soft, somewhat scanty fur'. The longer guard hairs were described by him as black or blackish and the body hairs as having a leaden greyish tint on the basal portion and a brown terminal portion which, in many hairs, was a bright brown tending to yellow. Thomas (1888) described the colour as 'finely grizzled rusty orange-grey, the orange deepest on the back, less on the belly, scarcely perceptible on the head and limbs'. No specimens examined in the course of this study could be described as golden or orange nor could any of the body hairs be described as yellow. It seems likely that these discrepancies are due to the means of preservation, since leaching of colour has been observed in specimens preserved for long periods in alcohol in the collection of the Queensland National Parks and Wildlife Service.

Owen (1879) and Carlsson (1915) briefly mentioned the facial and ulnar carpal vibrissae. Heighway (1939) provided a more detailed description which is largely confirmed by details of adults in the Pallarenda collection. Table 5 compares data from these with the findings of Heighway and with those of Lyne (1959) of *Potorous tridactylus*, *Bettongia gaimardi* and *Macropus giganteus*. The pattern of distribution and number of vibrissae is not very different from that of the Potoroinae but the presence of three groups of vibrissae on the forelimbs is a condition not found in other macropods. Suborbital and rhinal vibrissae, characteristic of kangaroos and wallabies (Lyne, 1959) are absent.

DESCRIPTION AND BIOLOGY OF *HYPSIPRYMNODON*

TABLE 5. Numbers of vibrissae in *Hypsiprymnodon moschatus* and other macropods. Data on *Hypsiprymnodon moschatus* from Heighway (1939); on *Potorous tridactylus*, *Bettongia gaimardi* and *Macropus giganteus* from Lyne (1959).

Vibrissae (each side)	<i>Hypsiprymnodon moschatus</i>	<i>Potorous tridactylus</i>	<i>Bettongia gaimardi</i>	<i>Macropus giganteus</i>
Mystacial	12-14	10-13	10-13	7-15
Supraorbital	2	2	3-5	4-8
Genal	3	1-2	2	2-5
Submental	indef.	indef.	indef.	indef.
Interramal*	2	1-2	2	1-3
Anconeal	1	0	0	0
Medial antebrachial	1	0	0	0
Ulnar carpal	2	1-4	1-4	1-2

* Includes *all* vibrissae in group.

In contrast to bettongs and potoroos, *Hypsiprymnodon* has a manus that is not specialised for digging. The digits radiate from the palm, as in most arboreal marsupials, and the claws function as hooks rather than as shovels. If, as earlier suggested, the first interdigital pad is fused with the thenar pad, all components of the primitive mammalian palm are present and the arrangement is remarkably unspecialised. The transverse striations of the pads provide resistance against slip while the animal is moving along a smooth surface and, when the digits are abducted towards the centre of the palm, the pads are opposed, providing a firm but flexible grip. In its general structure, the manus of *Hypsiprymnodon* resembles that of the arboreal burramyid *Cercartetus nanus*, differing from it mainly in the retention of sharp, curved claws.

As can be seen in Fig. 10, there is much less disproportion between the fore- and hindlimbs of the Musky Rat-kangaroo than in typical macropods. The relative lengths of the skeletal elements of the limbs are compared with those of some possums and macropods in Table 6, which demonstrates that, in many respects, the limb proportions resemble those of typical possums rather than typical macropods. This similarity is seen in the length of the fore- and hindlimbs, expressed as a proportion of the body length, and in the length of the forelimb expressed as a proportion of that of the hindlimb. Expressed as a proportion of the body length, the pes is notably more elongate than in possums but somewhat less than in other macropods; expressed as a proportion of the combined length of the femur and tibia, it is intermediate between possums and typical macropods.

If, as seems reasonable, this somewhat arbitrary series of possums and macropods represents increasing adaptation to saltation, it is interesting to note that reduction in the length of the forelimbs is due mainly to shortening of the proximal element (the humerus being 27% of the length of the presacral vertebral column in *Trichosurus vulpecula* and *Pseudecheirus peregrinus*, 26% in *H. moschatus*, 17-20% in the two potoroines and 19% in *Macropus robustus*). Increase in the length of the hindlimb is mostly the result of elongation of the

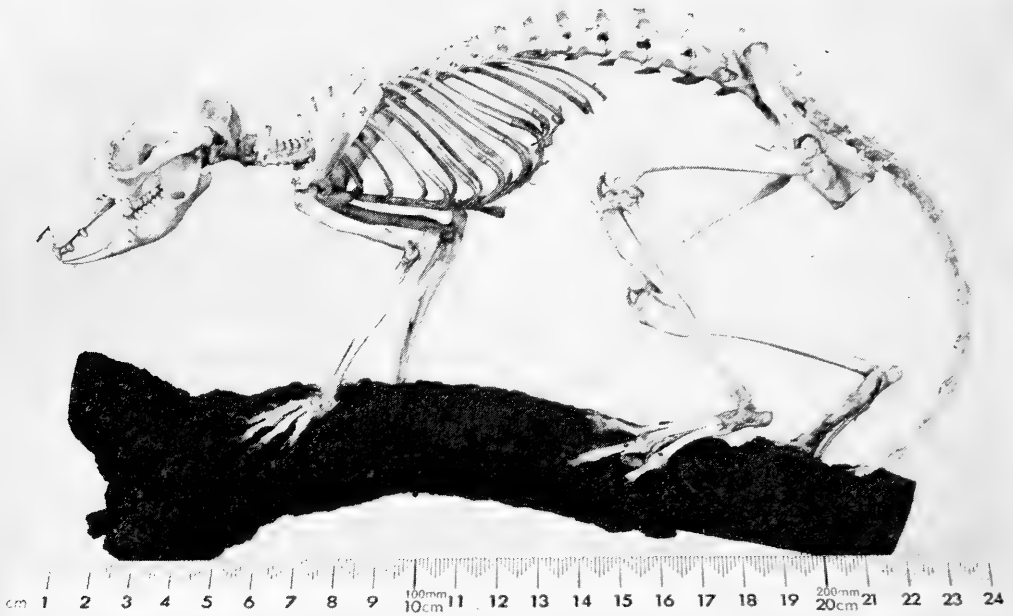


Fig. 10. Mounted skeleton of *Hypsiprymnodon moschatus* (AM, uncatalogued). Tail and fifth digit of hind foot are incomplete.

distal elements. The tibia is 31-36% of the length of the presacral vertebral column in the two possums, 46% in *H. moschatus*, 43-56% in the two potorines, and 68% in *M. robustus*. Relative length of the pes increases from 29% in the possums to 58% in the kangaroo.

Similarities between the limb proportions of *Hypsiprymnodon* and *Dendrolagus bennettianus* are of interest in that the latter demonstrates a secondary adaptation to an arboreal way of life. The evolutionary plasticity of macropods is indicated by the fact that the limb proportions of this tree-kangaroo are closer to those of possums than to *Hypsiprymnodon*, a fact which raises the possibility that the condition seen in *Hypsiprymnodon* could also be the result of a secondary adaptation. However, when viewed in the context of its other unspecialised characters, it seems much more likely that the Musky Rat-kangaroo is representative of an early stage of evolution of macropods from an arboreal, possum-like stock.

The unique presence of a hallux and the lack of hypertrophy of the fourth digit are characters that have been cited as primitive ever since Owen's (1879) description of the foot but the significance of the pedal pads warrants further

TABLE 6. Length (in mm and as proportion of length of presacral vertebral column, L/PS) of skeletal elements of limbs of single specimens of various marsupials. F, femur; F+T, femur + tibia; H, humerus; H+R, humerus + radius; L/PS, length of element divided by length of presacral vertebral column; M, manus; P, pes; PS, presacral vertebral column; R, radius; T, tibia.

	<i>Trichosurus vulpecula</i>		<i>Pseudocheirus peregrinus</i>		<i>Hypsiprymnodon moschatus</i>		<i>Potorous tridactylus</i>		<i>Bettongia lesueur</i>		<i>Macropus robustus</i>		<i>Dendrolagus bennettianus</i>	
	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS	mm	L/PS
PS	330	1.00	173	1.00	140	1.00	210	1.00	201	1.00	415	1.00	405	1.00
H	88	0.27	46	0.27	37	0.26	41	0.20	34	0.17	78	0.19	102	0.25
R	97	0.29	46	0.27	43	0.31	48	0.23	41	0.21	117	0.28	107	0.26
H+R	185	0.56	92	0.53	80	0.57	89	0.42	75	0.37	195	0.47	209	0.52
M	62	0.19	33	0.19	28	0.20	47	0.22	30	0.15	—	—	76	0.19
F	110	0.33	61	0.35	58	0.41	82	0.39	89	0.44	163	0.39	146	0.36
T	103	0.31	62	0.36	65	0.46	91	0.43	111	0.56	282	0.68	148	0.37
F+T	213	0.64	123	0.71	123	0.88	173	0.82	200	0.95	445	1.07	294	0.73
P	96	0.29	50	0.29	60	0.43	92	0.44	116	0.58	240	0.58	143	0.35
H+R F+T	0.87		0.75		0.65		0.51		0.38		0.44		0.71	
P F+T	0.45		0.41		0.49		0.53		0.58		0.54		0.49	

comment. These have a primitive configuration, being arranged essentially as in *Didelphis*, *Phascogale* or *Cercartetus* and, as in these arboreal animals, the transverse striations appear to be an adaptation to climbing. The elongate hypothenar pad is a raised surface against which the first interdigital and/or thenar pad is opposed when the first digit is abducted, thus providing a grip between the first and second digits but, as mentioned earlier, the extent which *Hypsiprymnodon* utilises the hallux and sole pads to grip a branch has not been determined.

Although many points of resemblance may be found between the skull of *Hypsiprymnodon* and those of one or other of the Potoroinae, there are few which enable it to be linked with this group in clear distinction from other macropods. Pearson (1950b) has pointed out that, in potoroines, the alisphenoid and parietal have a wide contact in the temporal region of the cranial roof. In *Hypsiprymnodon*, however, there is a very short fronto-squamosal contact which slightly separates the parietal from the alisphenoid, while in the Potoroinae (or most potoroines, see below) the fronto-squamosal contact is a quite significant suture and the parietal does not approach the alisphenoid. Pearson interpreted these facts as indicating separate evolutionary origins of his family Potoroidae (*Hypsiprymnodon* plus Potoroinae) and his Macropodidae (all other macropods). On this interpretation, *Hypsiprymnodon* is close to the potoroine stem but the fact that the parietals and alisphenoids are sometimes in contact on one or both sides of the skull of *Bettongia lesueur* weakens his argument. It does not, however, detract from his postulated close relationship between *Hypsiprymnodon* and the Potoroinae.

The quadritubercular molars and blade-like premolars of *Hypsiprymnodon* resemble those of Potoroinae on the one hand and those of *Burramys* on the other but Ride (1961) has argued persuasively that the burramyid and hypsiprymnodontine conditions have been attained independently. On dental characteristics, however, it is reasonable to assume a common ancestry for *Hypsiprymnodon* and the Potoroinae and the retention of rudimentary second incisors in *Hypsiprymnodon* suggests that, in this respect, it is more primitive than the Potoroinae.

Pearson (1945, 1950a, 1950b) concluded that the female urogenital system of *Hypsiprymnodon* and the Potoroinae is far more specialised than that of other macropods in having an enlargement of the anterior region of the vaginal complex, fusion of the posterior parts of the two lateral vaginae to form a posterior vaginal sinus, a short urogenital sinus and an extremely anterior attachment of the urinary bladder. In respect of all these characters, he regarded *Hypsiprymnodon* as the least specialised member of his family Potoroidae. The fact that *Hypsiprymnodon* normally rears two young simultaneously may also be interpreted as a primitive aspect of its reproduction.

Like the Potoroinae, *Hypsiprymnodon* is omnivorous but it is even less adapted to the mastication and digestion of cellulose fibre than these animals.

DESCRIPTION AND BIOLOGY OF *HYPSIPRYMNODON*

As demonstrated by Carlsson (1915) and Heighway (1939), the stomach is unsacculated, being indistinctly divided into cardiac, oesophageal and pyloric regions, and the caecum is short. It is reasonable to interpret this as evidence of descent from a frugivorous and/or insectivorous ancestor.

There is much evidence for a common evolutionary origin of *Hypsiprymnodon* and the Potoroinae but where the origin is to be found among the diprotodonts remains uncertain. Within the macropods, the simplistic idea of a linear progression (*Hypsiprymnodon* — Potoroinae — Macropodinae) cannot be supported. Moreover, as Ride (1971, 1978) has shown, Bensley's (1930) hypothesis of a diphyletic origin of the rat-kangaroos (whereby a primitive phalangerine stock gave rise, on the one hand to a *Hypsiprymnodon* — *Bettongia* — *Aepyprymnus* lineage and, on the other, to a macropodine radiation of which *Potorous* and *Caloprymnus* were early offshoots) suffers from the attempt to put modern forms into an evolutionary sequence. His hypothesis is also based on suspect dental homologies. Ride (1978) finds much in favour of the view of Winge (1893-1941), who decisively separated *Hypsiprymnodon* and all the Potoroinae from the Macropodinae. Expressed in contemporary taxonomic terms, Winge's hypothesis is that an ancestral arboreal phalangerid-like stock (his Phalangistini) gave rise, on the one hand to the relatively unspecialised Phalangeridae and the more specialised Burramyidae and Tarsipedidae and, on the other, to the Macropodidae. The Macropodidae was seen by him as consisting of two lineages, the Macropodinae and a *Hypsiprymnodon*-potoroine group, each of which may have had a separate origin from the basal Phalangistini.

Among these theories, we incline to the views of Winge and Ride. Although *Hypsiprymnodon* retains a significant array of characters that appear to be retained from a pre-macropod ancestor, it is not sufficiently different from potoroinae to justify a tripartite division of a family Macropodidae into sub-families Hypsiprymnodontinae, Potoroinae and Macropodinae. The probable relationship between these sub-groups is better represented by elevation of the macropods to a superfamily Macropodoidea comprising the families Potoroidae (Hypsiprymnodontinae and Potoroinae) and Macropodidae (Sthenurinae and Macropodinae), as proposed by Pearson (1950b), Archer and Bartholomai (1978) and Szalay (1982).

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A Review of the Genus *Myersina* (Pisces: Gobiidae), with the Description of a New Species

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ABSTRACT

The genus *Myersina* is characterised, and the type species, *Myersina macrostoma*, re-described from the holotype and recently collected specimens from Japan. *Myersina lachneri* is described as a new species based on four specimens from New Britain.

INTRODUCTION

Approximately 500 gobioid genera have been described, and between 200 and 300 are probably distinct (Hoesé, unpublished). Unfortunately in many cases the genera have not been adequately described and the type species often have not been figured. A large percentage of the described genera have not been revised or treated in any major work on gobioid fishes. As a result taxonomists have generally been frustrated in attempting to identify gobioid fishes. Many of the Indo-west Pacific genera have been regarded as monotypic. Recent studies are indicating that few monotypic gobioid genera exist. Relatively few of the monotypic genera previously recognized resulted from deliberate splitting of closely related forms. In most cases early workers were simply unaware that a genus had been described previously or lacked sufficient comparative material. In many cases incorrect generic placement of described species has also contributed to the apparent high degree of monotypy. Finally, the more intensive collecting effort in recent years has revealed undescribed species in genera thought to be monotypic.

In the present study we redefine the genus *Myersina*, a poorly known gobioid genus found in burrows in shallow waters of the western Pacific. The genus is shown to contain two species, *M. macrostoma* Herre and *M. lachneri*, n. sp.

Counts and measurements of the fish follow those given by Hubbs and Lagler (1958) and Hoesé and Steene (1978). The transverse scale count is taken from the anal fin origin upward and backward to the base of the second dorsal fin. The term transverse in relation to the sensory papillae patterns refers to both vertical and transverse rows as is standard in gobioid descriptions.

Material for this study is deposited in the following institutions: Australian Museum, Sydney; AMS. British Museum (Natural History); BMNH. Stanford University collection housed at the California Academy of Sciences, San Francisco; SU. Yokosuka City Museum, Japan; YCM.

Myersina

Myersina Herre, 1934: 89 (type species: *Myersina macrostoma* Herre, 1934, by original designation).

DIAGNOSIS

Gill membranes connected to form a distinct fold across isthmus under a point between eye and posterior preopercular margin, attaching to isthmus below eye. Vomer protrudes ventrally into mouth, anterolateral margins enlarged, with fleshy lobes. Sensory papillae on cheek in several short transverse rows radiating from eye; transverse rows under eye not extending below longitudinal row, which extends posteriorly from near posterior end of jaws. Mandibular papillae in two parallel longitudinal rows on chin. Outer row of teeth enlarged in both jaws. A pair of enlarged posteriorly directed teeth near middle of upper jaw in posterior-most row. First dorsal fin high, greater than body depth, with some rays prolonged. Dorsal origin slightly behind pelvic origin. Jaws reaching to below middle to end of eye. Body higher anteriorly, tapering posteriorly. Head laterally compressed. Numerous elongate rakers on outer face of first gill arch. Scales cycloid. First

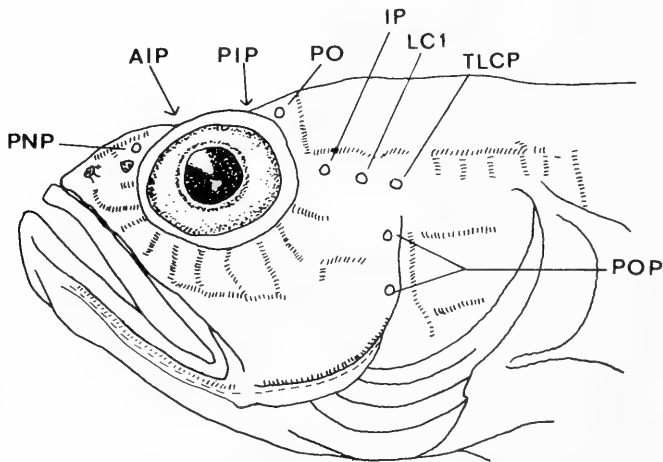


Fig. 1. Sensory papillae and head pores in *Myersina lachneri*, based on holotype and paratypes. Anterior interorbital pore, AIP; posterior nasal pore, PNP; posterior interorbital pore, PIP; postorbital pore, PO; infraorbital pore, IP; lateral canal pore, LC1; terminal lateral canal pore, TLCP; preopercular pores, POP.

A REVIEW OF THE GENUS MYERSINA

dorsal fin rays VI. Second dorsal fin rays I, 10. Anal fin rays I, 9-10. Pectoral fin rays 15-16. Longitudinal scale count 45-55. Transverse scale count 15-23. Gill rakers on outer face of first arch 5-6 + 1 + 16-19. Head pores: a posterior nasal pore adjacent to each posterior nostril; a median anterior interorbital pore present or absent; a median posterior interorbital pore above end of eye; a post-orbital pore behind each eye; an infraorbital pore below each postorbital pore; a lateral canal pore behind each infraorbital pore (absent in one specimen of *M. lachneri*); and a terminal lateral canal pore above posterior preopercular margin; two (or rarely 3) preopercular pores (Fig. 1).

DISCUSSION

This genus was originally described as having flat vomerine teeth (Herre, 1934). As noted by Akihito and Meguro (1978), there are no vomerine teeth, but there is a fleshy lobe at each side of the front of the vomer, which can be mistaken for a tooth.

The relationships of *Myersina* are at present uncertain. Akihito and Meguro (1978) suggest a possible relationship with *Cryptocentrus*, but the gently sloping snout, development of numerous elongate gill rakers, and the formation of a free fold across the isthmus by the branchiostegal membranes suggest that the relationship may not be close. The membrane across the isthmus is uncommon in gobiids, but occurs in *Stonogobiops* (Polunin and Lubbock, 1977). *Stonogobiops* has true vomerine teeth, a blunt snout, and short gill rakers. The relationships of these genera are under study by the senior author.

Currently only two species of *Myersina* are known. These have been collected from burrows in mud in mangrove lagoons, and from a reef.

KEY TO SPECIES

1. Anterior interorbital pore usually absent. A lateral stripe on body and no distinct transverse bands. No scales in front of a line from upper pectoral base origin to or just behind sixth dorsal spine. Anal rays usually I, 9. Japan and Philippines *M. macrostoma*
1. Anterior interorbital pore present. A lateral stripe on body and 6 or 7 distinct transverse bands. Scales extending forward to under third dorsal spine. Anal rays I, 10 *M. lachneri*, n.sp.

Myersina lachneri n.sp.

(Figs 1 and 2)

DIAGNOSIS

Second dorsal and anal fin rays I, 10. Anterior interorbital head pore present. Caudal fin pointed in both sexes. Body partly scaled, with scales extending forward to below a line from third dorsal spine of first dorsal fin to pectoral base. Head naked. Body with 6 or 7 vertical bands.



Fig. 2. Holotype of *Myersina lachneri* (preserved).

DESCRIPTION

Based on 4 specimens, 22-26 mm SL. Counts and measurements are given in Table 1. Branchiostegal rays 5 (in 2). Vertebrae 10 + 16 (in holotype). Head strongly compressed, cheeks not bulbose. Snout shorter than eye length, gently sloping in lateral view, with snout tip in horizontal line from middle of eye. Eye 3.0-3.4 in head. Interorbital very narrow, less than pupil diameter. Mouth large, oblique, forming an angle of about 40° with body axis; jaws end under a point below middle to posterior half of pupil. Gill rakers on outer face of first arch slender and elongate, longer than gill filaments ventrally. Rakers on inner face of first arch and both faces of other three arches developed as short knobs. First four dorsal spines greatly elongated, second or third spine longest, reaching to above posterior end of second dorsal fin to above base of caudal when depressed. Fifth dorsal spine shorter than others, only slightly elongated. Sixth dorsal spine widely separated from fifth, and short and not prolonged. Pectoral rays branched except for uppermost and lowermost rays. Posterior margin of pectoral fin obtusely rounded, reaching to above anal origin. Pelvic disc large, reaching to below second or third anal ray. Caudal tip pointed in both sexes; segmented rays 8-10 (from top) longest; ray 9 produced into short filament in single female. Body covered with cycloid scales, except for two naked anterior

A REVIEW OF THE GENUS MYERSINA

patches, one extending forward from below second dorsal spine to upper pectoral fin base, and the second from just before anus to behind middle of pectoral fin base. Midline of belly naked. Nape and head naked. Urogenital papilla of male long and with pointed tip; broad and blunt-tipped in female.

TABLE 1. Counts and measurements (in mm) of types of species of *Myersina*.

	<i>M. macrostoma</i>		<i>M. lachneri</i>		
	Holotype SU 26770	Holotype BMNH	BMNH	Paratypes AMS	AMS
Sex	♂	♂	♂	♂	♀
First dorsal	VI	VI	VI	VI	VI
Second dorsal	1,10	1,10	1,10	1,10	1,10
Anal	1,9	1,10	1,10	1,10	1,10
Pectoral	16	16	15	16	16
Segmented caudal	17	17	17	17	17
Branched caudal	—	14	13	—	14
Longitudinal scale count	55	51	45	48	50
Transverse scale count	23	20	21	—	18
Gill rakers on outer face of first arch	6+1+19	6+1+17	6+1+16	6+1+19	5+1+16
Standard length	18.7	25.7	22.2	24.7	26.0
Head length	6.2	7.9	6.4	7.2	7.7
Head depth at preopercular margin	4.0	5.4	4.5	5.2	5.1
Head width at preopercular margin	3.1	3.8	3.2	3.7	3.6
Snout length	1.1	1.9	1.5	1.7	1.6
Eye length	2.0	2.3	2.9	2.4	2.4
Suborbital width	0.4	0.5	0.4	0.6	0.5
Predorsal length	7.2	9.4	8.6	8.8	9.5
Preal anal length	10.6	14.5	12.6	14.9	15.1
Prepelvic length	6.0	7.4	6.9	6.9	6.9
Pectoral length	4.8	6.8	6.0	7.0	6.5
Pelvic length	4.2	7.9	6.9	6.9	6.9
Depressed dorsal length	8.3	19.2	14.2	14.5	18.7
Third dorsal spine length	7.2	19.0	14.0	14.5	18.5
Body depth at anal origin	3.7	5.1	4.2	4.9	4.9
Caudal peduncle length	3.8	4.6	4.9	4.8	5.2
Caudal peduncle depth	2.3	2.9	2.6	2.7	2.9

COLOURATION IN ALCOHOL

Head and body brown. Faint dark brown stripe extending back from posterior margin of eye, expanding into large brown spot covering upper half of operculum. Stripe continues on body from behind pectoral fin base and above midside anteriorly and sloping slightly downward, crossing midside below end of second dorsal fin, and reaching below midside on caudal peduncle; extending to end of caudal fin below midline of fin, and expanding ventrally to cover most of lower half of caudal fin. Body with 6 or 7 vertical bars, width about equal to eye diameter; bars slightly oblique, sloping downward and forward; 2 bars under first dorsal fin, 4 bars under second dorsal fin, and sometimes a bar on caudal peduncle; posterior 3 bars faint in female. All fins except pectoral dusky

to dark brown. Membrane between first two dorsal spines black, darkest near body; a dark diffuse mark on membranes from behind fourth dorsal spine to end of fin. Second dorsal fin with a light grey stripe just above body; distal margin of fin clear or light grey and an elongate dark brown mark on membrane between successive rays. Female also with a light central area between rays, extending parallel to rays. Upper posterior half of caudal fin with clear margin, followed below with a very faint grey stripe, followed by a thin clear area. Pectoral fin clear to light brown.

DERIVATION OF NAME

For Dr. Ernest Lachner, in recognition of his contributions to systematics of gobioid fishes.

Material Examined: Holotype — BMNH 1980.5.21:1, a 25.7 mm SL male, in mud burrows at 1-2 m depth, Blanche Bay, New Britain, Papua New Guinea. Paratypes — AMS I. 20831-001, 2(24-26 mm SL), and BMNH 1980.5.21:12, 1(22 m SL), taken with holotype.

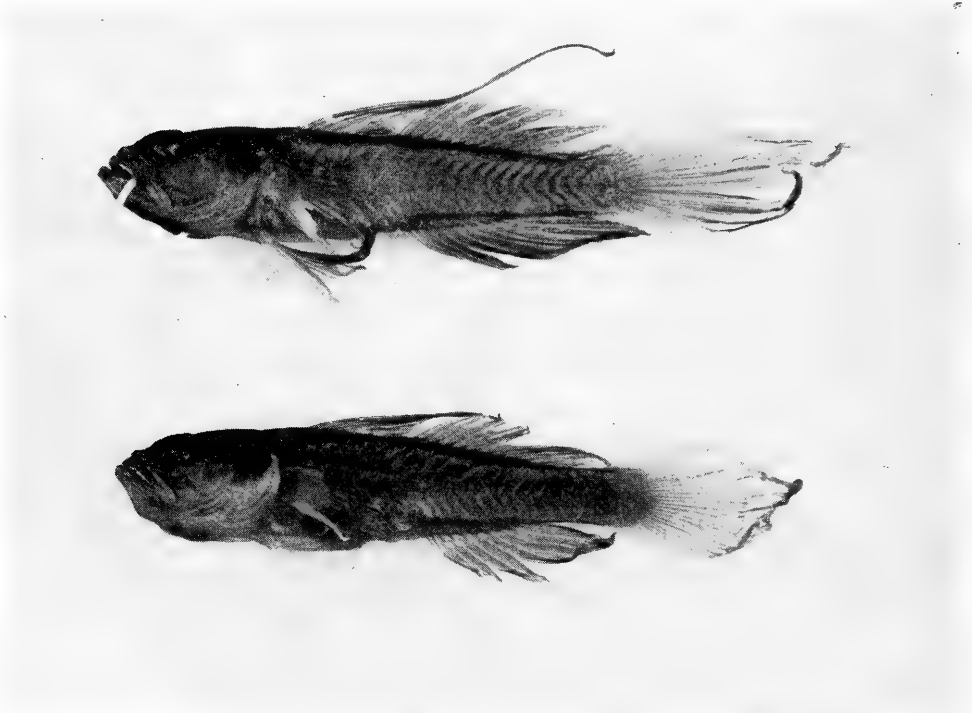


Fig. 3. *Myersina macrostoma* male (upper) and female (lower) from Japan (preserved). Note caudal fin damaged in both specimens and shape differences not apparent.

Myersina macrostoma

(Figure 3)

Myersina macrostoma Herre, 1934: 90 (Culion Harbour, Philippines). — Akihito and Meguro, 1978: 295 (Japan).

DIAGNOSIS

Second dorsal fin rays typically I, 10. Anal fin rays usually I, 9. Anterior interorbital head pore usually absent. Caudal fin pointed or with an obtusely rounded margin in females, truncate in males. Body scales reduced, with scales extending forward in a wedge from end of base of first dorsal fin to behind pectoral base. Belly naked. Body with a distinct horizontal stripe from behind eye to caudal base and no vertical bands.

COLOURATION IN ALCOHOL

Based on male and female from Japan (YCM 2632-5 and YCM 2632-8). Head and body light brown. A large brown spot covering upper half of operculum. A faint broad brown stripe extending from end of eye to base of caudal fin. Median fins dusky. First dorsal fin with an elongate black mark covering membrane between first two dorsal spines from just above base, fading dorsally. Second dorsal fin with four rows of faint brown oval spots, slightly smaller than pupil. A faint blackish spot around middle of sixth dorsal spine. Anal fin dusky, becoming darker near distal tip in male. Caudal fin dusky, darker below in male. Pectoral fins clear. Pelvic disc dusky, darker posteriorly in male.

HOLOTYPE

The holotype of *Myersina macrostoma* was compared with the two specimens from Japan. Data on additional material from Japan was kindly provided by His Imperial Highness, the Crown Prince of Japan and Mr. K. Meguro. The holotype has the body scales extending along the back to below the sixth dorsal spine and then continues obliquely to just behind the pectoral base, leaving a large naked wedge under most of the first dorsal fin. Akihito and Meguro (1978) recorded a lateral scale count of 62, but recounting gives a count of 55. In Japanese material the scale count ranges from 51 to 55, while in *M. lachneri*, the count is from 48 to 51. However, too few specimens are available to determine if the difference is significant. Similarly, the upper jaw reaches to the end of the eye (15.5% of SL) in holotype, while in the males from Japan the jaw length varies from 16.1 to 18.7% of SL, but the holotype is considerably smaller than the other material. Males of similar size in *M. lachneri* have a jaw length of 12.8 to 14.9% of SL, and the jaw ends under the posterior half of the pupil. In the holotype of *M. macrostoma*, the anterior interorbital pore is absent, and the anal ray count as well as other meristics agree with Japanese material. Although the colouration of the holotype has faded, Herre (1934) mentioned the horizontal

stripe, but did not indicate any vertical bars. He indicated that the stripe continues onto the upper part of the caudal fin, but the caudal fin is darkest ventrally in the preserved holotype. In Japanese material the whole caudal is dark, but generally darkest ventrally in males. The tip of the caudal fin is broken off in the holotype.

DISCUSSION

This species has recently been redescribed by Akihito and Meguro (1978). The papillae and head pores are similar to *M. lachneri*, but the anterior interorbital pore is usually absent, although present in 2 of the 9 Japanese specimens. Generally *M. macrostoma* has 2 preopercular pores, but one Japanese specimen has 3 pores on both sides and two have 3 pores on one side and 2 on the other.

This species has been collected from a reef in the Philippines and from mangroves in burrows in Japan.

MATERIAL EXAMINED

Holotype, SU 26770, an 18.7 mm SL male, Culion Harbour, Philippines. YCM 2632-5 and -8, 2(35-36), mouth of Shiu River, Magura, Ishigakijima, Okinawa Prefecture, Japan.

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***Ventrifossa johnborum*, a New Grenadier from the Western Pacific (Macrouridae: Pisces)**

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ABSTRACT

Ventrifossa johnborum is described from four specimens collected in the Bismarck Sea, Philippines, and the South China Sea. The new species is closely related to *V. misakia* Jordan and Gilbert from Japan, and the two constitute the sole members of sub-genus *Sokodara* Iwamoto, 1979.

INTRODUCTION

Paxton and Lavenberg (1973) reported on an anglerfish (*Diceratias hispidus*) that apparently died from attempting to eat a prey much larger than itself. The prey was a grenadier of the genus *Ventrifossa*, which they noted "does not match the description of any species described by Gilbert and Hubbs (1920) and Parr (1946)," but they were reluctant to formally name it because of the deteriorated condition of diagnostic characters resulting from partial digestion. My particular interest in this genus of grenadiers prompted me to borrow the specimen to determine its identity. The specimen appeared to be closest to *V. misakia* (Jordan and Gilbert, 1904), a species not previously known from the vicinity of the Bismarck Sea and, in fact, reported only once from outside Japan. That single record of *V. misakia* was based on a small, poorly preserved individual from the Philippines, which Gilbert and Hubbs (1920:545) compared with the holotype and noted that "certain differences . . . render somewhat doubtful the reference of [the] specimen to *V. misakia*. The snout is longer; the barbel much longer; the distances greater between the anus and the origin of the anal fin and between the ventral base and the isthmus;" than normally occurs in *V. misakia*. These characters, for the most part, appeared to distinguish not only the Philippine specimen, but also the Bismarck Sea specimen and two others I had previously examined from the South China Sea, from representatives of *V. misakia* from Japan. Based on these and other characters

enumerated below, the specimens are recognised as representing a new species, and hereafter are called *Ventrifossa johnboborum*. This species and *V. misakia* can be differentiated by the characters given in the following key:

- 1a. Oral cavity pale. Barbel 4-8 percent of head length (HL); interorbital width 30-35 percent HL; interspace between first and second dorsal fins 40-62 percent HL; distance anus to anal origin 11-15 percent HL; Japan *Ventrifossa misakia*
- 1b. Oral cavity blackish. Barbel 11-16 percent HL; interorbital width 28-30 percent HL; interspace between first and second dorsal fins 37-41 percent HL; distance anus to anal origin about 20 percent HL; Philippines, South China Sea, Bismarck Sea *Ventrifossa johnboborum*

MATERIALS AND METHODS

Methods of making counts and measurements follow procedures outlined in Iwamoto (1970). Abbreviations used in reference to study material include: AMS, Australian Museum, Sydney; FRSA, Fisheries Research Station, Aberdeen, Hong Kong; USNM, United States National Museum of Natural History, Washington, D.C.

STUDY MATERIAL

Holotype. AMS No. I. 15602-002, Bismarck Sea, floating at surface near Tanga Island, Papua New Guinea, 30 Apr. 1967 [in mouth of anglerfish *Diceratias bispinosus*].

Other material. USNM 149044 (32 mm HL, 70 + mm TL); off Atalaya Pt., Batag Island, Luzon, Philippines, 12°44'42"N, 124°59'50"E, Albatross sta. 5445, (depth approximately 702 m), 3 June 1909. — FRSA, uncat., 1 specimen, 75 mm HL, 320 + mm TL, South China Sea (depth 732-796 m), cruise 1/64, sta. 26, 7 Jan. 1964. — FRSA uncat., 1 specimen, 48 mm HL, 185 + mm TL, South China Sea, cruise 4/64, sta. 19, 5 Mar. 1965.

Specimens from the South China Sea are not included as type material because information on these is based on sketchy notes taken in 1970 during a brief visit to the Fisheries Research Station, Aberdeen, and also because a permanent disposition of the specimens could not be assured. The Luzon specimen is in poor condition and is so much smaller than the holotype that differences in morphometry (especially the snout and suborbital region) may indicate more than ontogenetic variation. Without adequate size series, these differences could not be adequately evaluated.



Fig. 1. *Ventrifossa johnborum* n. sp. Holotype, AMS No. I.15602-002, from the Bismarck Sea. Lateral and dorsal views, and enlarged view of scale taken from below origin of second dorsal fin. Drawn by Beth Meinhard.

***Ventrifossa johnborum* n. sp.**

(Figure 1)

Ventrifossa misakia (non Jordan and Gilbert, 1904): Gilbert and Hubbs, 1920:545-546 (one specimen, Batagia I., Philippines). Roxas and Martin, 1937:63 (compiled Philippine record). Herre, 1953:1974 (compiled Philippine record).

Ventrifossa sp.: Paxton and Lavenberg, 1973:47-50, fig. 1 (one specimen in mouth of anglerfish *Diceratias bispinosus* found floating on surface, Bismarck Sea).

DIAGNOSIS

A broad-headed species of *Ventrifossa*, subgenus *Sokodara* (as defined by Iwamoto, 1979), with 8-9 pelvic fin rays. Lining of oral cavity blackish. Interorbital width 28-30 percent of HL. Barbel small, 11-16 percent HL. Scales small

and finely spinulated (see Fig. 1) with slender, conical to somewhat lanceolate spinules arranged in widely divergent "V" rows; about $9\frac{1}{2}$ to $10\frac{1}{2}$ rows from origin of second dorsal fin to lateral line; about 65-71 lateral line scales counted from origin over distance equal to predorsal length. Suborbital shelf very narrow anteriorly, 1-2 scale rows wide at narrowest point. Snout blackish at extreme tip, paler along leading edge; snout demarcated by a small, blunt, unilateral, tubercular scale. Inner gill rakers on first arch 12-14 total.

DESCRIPTION

Counts and measurements (holotype followed by range in other specimens in parentheses).

Counts — first dorsal rays II, 11 (8-10); pectoral rays 24 (20-23); pelvic rays 9 (8). Gill rakers on first arch 9 or 10 (lateral), 1 + 11 (mesial) (2 + 12); on second arch 2 + 10 (mesial) (2-3 + 11-12). Scales below origin of first dorsal about 20 (about 14-15); below midbase of first dorsal about 11; below origin of second dorsal $10\frac{1}{2}$ ($9\frac{1}{2}$); over distance equal to predorsal length about 65 (about 71 in USNM 149044). Pyloric caeca about 65. Abdominal vertebrae 15 (14 in USNM 149044).

Measurements — Total length 360 + mm (170-320 mm); head length 85.2 mm (32-75 mm). The following are given as a percent of head length: snout length 28 (29-31); preoral length 20 (23-25); greatest orbit diameter 31 (29-35); interorbital width 30 (28-30); postorbital length of head 41 (41-42); orbit to angle of preopercle 42 (42-45); suborbital width 12 (12-17); length upper jaw 42 (36-39); barbel length 16 (11-12); length outer gill slit 27 (14-21); preanal length 135 (136 in USNM 149044); base of outer pelvic ray to origin of anal fin 49 (36 in USNM 149044); greatest body depth 75 (76 in FRSA spec.); interspace between dorsals 41 (37); height of first dorsal fin about 60 (60-63); length pectoral fin about 446 (38-49 in FRSA spec.); length pelvic fins estimated 34 (29-41 in FRSA spec.).

Description of Holotype: (see Fig. 1)

Snout broadly pointed, moderately produced, and uniformly covered with small scales (evenly and completely covering surfaces). A small, conical, tubercular scute developed at apex of snout; scute not markedly different from surrounding scales. Dorsal profile low; nape barely rises above uppermost level of head; dorsal fin base almost flush with profile posteriorly. Suborbital shelf very narrow anteriorly, two small scales wide at narrowest point, but shelf broadens rapidly posteriorly. Gill openings wide. Branchiostegal membranes narrowly joined across isthmus at a point situated ventrad to posterior edge of orbits. Upper margin of preopercle inclined forward. Interopercle narrowly exposed along posteroventral margin of preopercle. Mouth large and broad; upper jaws extend posteriorly to vertical through posterior edge of orbits. Ascending limbs of premaxillae lean forward at a notably obtuse angle (much further inclined than in any other member of the genus except *V. misakia*). Lips thin and smooth (nonpapillaceous).

A NEW SPECIES OF GRENADIER

Scales extremely small, approaching both in size and spinulation those found in members of the genus *Malacocephalus*. Exposed margins of scales narrow and evenly covered with slender, relatively erect spinules arranged in widely divergent "V" rows. Spinules conical to somewhat flattened and lanceolate (but spinules mostly conical in smaller paratypes). Head and body completely covered with scales except on fins, lips, gill membranes, and periproct region.

Paired fins moderately large (for genus); outer pelvic ray essentially not prolonged beyond other rays of fin. Anal fin originates far forward on abdomen, about midlength of abdominal cavity, and about on vertical through hind margin of first dorsal fin. Serrations on spinous second ray of first dorsal fin rudimentary and confined to distal end; remainder of spinous ray smooth; ray not prolonged beyond succeeding rays (serrations on leading edge of spinous ray better developed in other specimens). Pelvic fins originate well forward of vertical through pectoral fin origin, below subopercle.

Jaw teeth all small, conical, and recurved to various degrees. Mandibular teeth in 2-3 irregular series laterally, in 3-4 series near symphysis. All mandibular teeth small, but inner series larger than more lateral ones. Premaxillary dentition in narrow band 4-5 irregular rows wide near symphysis, slightly narrower posterolaterally; outer series of teeth somewhat larger than inner series. A wide gap between opposite tooth bands at symphysis of upper jaw.

Ventromedian area of abdomen badly damaged in holotype, but in other specimens a small, oval anterior dermal window of ventral light organ is present. The blunter end faced posteriorly and is narrowly connected to periproct by a thin line of black skin. An indistinct posterior dermal window within periproct, before anus. Retia and gas glands two each, retia relatively short, broad, and flat.

Holotype a female with large, well-developed ovary on right side, but none developed on left side. Stomach contains three large squid beaks and other remains of squids. Pyloric caeca about 65, difficult to count, with many tips broken off; branching of caeca confined to or near bases.

Colouration in alcohol. Brownish overall with blackish or swarthy fins, lips, and gill membranes (USNM 149044 more pallid; tawny overall). Swarthy ventrally on trunk. Bluish on abdominal areas denuded of scales. Oral, pharyngeal, and branchial membranes blackish. Gill arches blackish, but filaments pale.

COMPARISONS AND RELATIONSHIPS

In addition to the differences between *V. misakia* and *V. johnboborum* noted in the key, *V. johnboborum* shows notable differences in the configuration of the suborbital ridge. That portion of the ridge below the anterior border of the orbits in *V. misakia* runs so close to the ventral orbital rim that it almost appears to touch the rim, being separated by only a single scale row at the closest

point. In *V. johnboborum*, however, the ridge line does not run as close, and there are two small scales separating the ridge line from the orbital rim. Furthermore, in the holotype of *V. johnboborum*, the second spinous dorsal ray appears to completely lack serrations on all but the distal one-quarter to one-third. In all specimens of *V. misakia* examined and in the USNM specimen of *V. johnboborum*, the ray had small, fine, but complete serrations on the leading edge.

Ventrifossa johnboborum and *V. misakia* form a closely related pair differentiated from other members of the genus by a combination of squamation features, configuration of the suborbital ridge, vertebral numbers, and retia-gas gland shapes. The two are considered to be the only members of the subgenus *Sokodara* (Iwamoto, 1979). *Ventrifossa nasuta* (Smith, 1936) from the Indian Ocean resembles *V. misakia* and *V. johnboborum* in general head and body shape, and in having a distinct terminal snout scute and a narrow suborbital shelf below the anterior part of the orbit, but *V. nasuta* has much larger, coarser scales (about 6-7 scale rows from origin of the second dorsal fin to lateral line).

DISTRIBUTION AND HABITS

Ventrifossa misakia is apparently confined to waters off Japan, whereas *V. johnboborum* ranges widely to the south of this in the Indo-Australian Archipelago. The new species was absent from the extensive trawl collections made off Australia and New Zealand by the Japanese research vessel *Kaiyo Maru* (Arai, *in litt.*, 1979).

Most *Ventrifossa* specimens are captured in bottom trawls, thus suggesting a primarily benthic or benthopelagic habit for the species. The presence of the holotype of *V. johnboborum* in the mouth of an anglerfish and the squid remains in the stomach of the holotype might initially suggest vertical forays into the water column by individuals of the new species. Okamura (1970:78) has, in fact, suggested vertical migrations in *V. garmani* based on hook-and-line captures of individuals off Japan, but in these hook-and-line captures, the baited hooks were set on drop lines attached to a vertical mainline, and the fish may well have "followed" the baited series of hooks vertically to the upper part of the mainline where they were caught (Okamura, pers. comm. 1971). Of more pertinence is Paxton and Lavenberg's (1973:50) statement that all (four) known metamorphosed females of *Diceratias bispinosus* were taken with bottom-fishing gear, and "apparently *D. bispinosus*, while having no obvious morphological adaptation for benthic life, lives and feeds close to the bottom." There is thus no reason to conclude that the *D. bispinosus* individual that captured the holotype of *V. johnboborum* did so other than near the bottom.

ETYMOLOGY

The species is named for John R. Paxton and Robert J. Lavenberg who first recognized the species as new.

A NEW SPECIES OF GRENADIER

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***Atherinosoma wallacei*, a new species of estuarine and inland water silverside (Teleostei: Atherinidae) from the Swan-Avon and Murray Rivers, Western Australia**

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ABSTRACT

Atherinosoma wallacei n.sp., is a common estuarine and inland water silverside or hardyhead having close affinities with the marine *Atherinosoma presbyteroides*. It is placed in *Atherinosoma* after examination of all the 18 existing type specimens representing the species found in this genus in Western Australia. Priority of *Atherinosoma* is confirmed.

INTRODUCTION

An annotated checklist of the fish fauna of the Swan-Avon River system in south-western Australia was compiled by Chubb *et al.* (1979) based on the records of the Western Australian Museum and a bi-weekly sampling programme at various sites within the estuary between February 1977 and March 1978. Identification of most teleosts posed few problems except for those of the Atherinidae. Although Chubb *et al.* tentatively listed two species for the genus *Atherinosoma*, namely *A. presbyteroides* (Richardson, 1843) and *A. elongata* (Klunzinger, 1879), subsequent work indicated that these designations were incorrect. A detailed study of the distribution, abundance and species composition of *Atherinosoma* within the Swan-Avon estuary was therefore initiated. It soon became evident that the problems posed in compiling the Swan-Avon checklist were due to the presence of an undescribed species which was closely related to the marine species *Atherinosoma presbyteroides*. This species is named *Atherinosoma wallacei* sp. nov. The taxonomic characters of this species and those of the other two species of *Atherinosoma* found in south-western Australia, namely *A. presbyteroides* and *A. elongata*, are compared.

TAXONOMIC BACKGROUND

Considerable confusion has existed over the generic status of several species of hardyheads or silversides in southern waters of Australia. As the work of

Ivantsoff (1978) has shown, this applies particularly to *Atherinosoma*, which is the predominant atherinid genus in this region. To understand the basis for placing the new species described in this paper in *Atherinosoma*, it is necessary to outline the problems surrounding the nomenclature of this genus and its species. A more detailed account of all the species in this genus is currently being prepared by one of us (W.I.).

Atherinosoma was erected as a monotypic genus by Castelnau (1872) to recognise the difference between his new species *Atherinosoma vorax* (of which no type specimens have survived) and species belonging to Northern Hemisphere atherinid genera. In 1895, Ogilby published a new name *Taeniomembras*, based on *Atherina microstoma* Günther, 1861. Ogilby's genus was accepted by subsequent workers such as McCulloch (1911) and Schultz (1948). Munro (1958), in his account of Australian atherinids, listed eight species in *Taeniomembras*. Without explanation, Whitley (1943) resurrected *Atherinosoma* Castelnau, 1872, to incorporate a number of species already placed in the genus *Taeniomembras* by Munro and other workers, including *Atherina microstoma*. A newly described species *Atherinosoma rockinghamensis* Whitley, 1943, and *Atherina elongata* Klunzinger, 1879, were also placed by Whitley (1943) in *Atherinosoma*. It appears that Whitley believed that *Atherinosoma vorax*, the type species of Castelnau's genus, was related to *Atherina microstoma* of Günther. Castelnau's (1872) clear account of *A. vorax*, especially the description of hooked teeth in jaws and the presence of teeth on the palatines and tongue, as well as a count of 36 scales along the mid-lateral line, leaves little doubt that *A. vorax* is the same as *Atherina microstoma*. This conclusion is supported by the fact that no other silverside species from Victoria and Tasmania, which are the type localities for the above mentioned nominal species, has fewer than 40 mid-lateral scales. The hooklike teeth in jaws, and teeth on the tongue and palatines, are typical of *A. microstoma*.

Atherina, an exclusively Northern Hemisphere genus, has been frequently used as a "catch-all" genus for the Australian species of silversides, especially those which are now included in *Atherinosoma*. *Atherina* differs from *Atherinosoma* in the skull roof morphology, in the shape of maxilla and by the presence of enlarged haemal arches. The two are therefore regarded as distinct. An investigation of Australian atherinids by Ivantsoff (1978) identified only three species that should be placed in the genus *Atherinosoma*, namely *A. microstoma*, *A. elongata* and *A. presbyteroides*.

The validity of the names *A. elongata* and *A. presbyteroides* requires some explanation. Examination of these types (Stuttgart Museum, S93, 2574C) demonstrated that *Atherina elongata* Klunzinger, 1879, is the senior synonym of *Atherinosoma edelensis* (*sensu* Whitley, 1955, 1958) and *A. rockinghamensis* (see Ivantsoff, 1978). However, the name *Atherinosoma elongata* (or *Taeniomembras elongatus*) has been used by some workers to describe an elongate hardyhead possessing greater than 15 gill rakers in the first lower gill arch, having a mid-

lateral scale count of 40-44 (Whitley, 1955, 1958; Munro, 1958) and having a long median premaxillary process. Since the osteological characters of *Atherinosoma elongata* used by Whitley and Munro do not agree with the type specimens of *Atherina elongata* (the types are in extremely bad condition), it is evident that the species described by them was an entirely different hardyhead.

The status of *Atherina presbyteroides* has been enigmatic since its description by Richardson in 1843. Although the types are lost, the description of this Tasmanian species specifies the premaxilla as not protractile and that there are 46 vertebrae and two rows of scales above the mid-lateral band. These characters make *A. presbyteroides* indistinguishable from *Atherina tamarensis* Johnston, 1883, *Atherinichthys edelensis* Castelnau, 1876, and *Taeniomembras elongata* (*sensu* Whitley, 1943).

MATERIALS AND METHODS

SOURCE OF MATERIAL

The specimens used in the description of *A. wallacei* came primarily from the Swan-Avon River system (Lat. 32°04', Long. 115°44') and to a lesser extent from the Murray River which flows into the Peel-Harvey estuarine system (Lat. 32°35', Long. 115°45'). The Swan-Avon River system has been defined by Jutson (1934) as comprising three rivers and their tributaries, namely the Swan-Avon, Helena and Canning. Sampling was carried out with beach seines in 1978, 1979 and 1980 (generally at least once monthly) at a number of sites in the lower, middle and upper estuary of the Swan-Avon complex (Chalmer, Hodgkin and Kendrick, 1976).

For a full description of the precise sampling method and the location of the sites see Chubb *et al.* (1981). Samples were also examined from Walyunga and Northam in the Swan-Avon located approximately 45 and 95 km respectively upstream from the mouth of the estuary. In the Peel-Harvey estuary, samples were obtained using the same techniques but at six weekly intervals during 1980. Specimens held by the Western Australian Museum (WAM) were also examined.

METHOD OF COUNTING AND MEASURING

The methods used for counts and measurements were modified from Munro (1967). The interdorsal scale count is taken from the origin of the last spine of the first dorsal fin to the origin of the first spine of the second dorsal fin along the mid-dorsal line. The number of transverse scales are counted from the origin of the first dorsal fin diagonally downwards and forwards to the upper edge of the mid-lateral band, plus those in the row of scales covering the mid-lateral band, plus the scales counted diagonally upwards and backwards from the origin of the ventral fins to the lower edge of the mid-lateral band. The predorsal scales are counted forwards from the first dorsal fin origin to the head so as to include all the scales in the mid-dorsal line. The position of the origin of the first dorsal

TABLE 1. Body measurements and counts of 30 specimens of *A. wallacei* from the Swan-Avon and Murray Rivers.

Abbreviations: SL, standard length; H max, greatest body depth; H min, least body depth of caudal peduncle; Sn, snout; OD₁, origin of first dorsal fin; OD₂, origin of second dorsal fin; OV, origin of ventral fins; TV, tip of ventral fins; OA, origin of anal fin; TA, last ray of anal fin; T Pec, tip of pectoral fins. Spines and unbranched rays are excluded in the counts for the elements of the second dorsal, anal and pectoral fins. Position of the fins and the anal aperture are expressed as the number of scales in front of (F) or behind (B) the point of reference where zero represents the point of reference.

Measurements and counts	Holotype	Mean, 1 standard deviation and range for holotype and 29 paratypes		
Standard length (SL) in mm	41.2	43.5	5.70	(30.7-54.1)
In SL				
Head	4.1	4.1	0.17	(3.7- 4.4)
H max	6.4	6.6	0.30	(5.9- 7.3)
H min	15.8	15.4	0.78	(13.5-16.9)
Sn-OD ₁	2.1	2.1	0.05	(2.0- 2.2)
Sn-OD ₂	1.5	1.4	0.04	(1.4- 1.5)
Sn-OV	2.5	2.4	0.09	(2.2- 2.5)
Sn-TV	1.8	1.8	0.05	(1.7- 1.9)
Sn-OA	1.5	1.5	0.04	(1.4- 1.5)
Sn-TA	1.2	1.2	0.05	(1.2- 1.3)
In head				
Eye	3.0	2.9	0.13	(2.7- 3.1)
Interorbital	3.9	3.9	0.19	(3.4- 4.3)
Postorbital	2.4	2.4	0.15	(2.1- 2.7)
In eye				
Snout	1.5	1.5	0.15	(1.2- 1.8)
Premaxilla	1.0	1.0	0.09	(0.8- 1.2)
Premaxillary process	1.8	2.0	0.24	(1.4- 2.4)
Scale counts				
Midlateral scales	39	39.0	0.83	(38-41)
Transverse scales	5.5	5.3	0.37	(5-6)
Predorsal scales	15	14.7	0.58	(14-16)
Interdorsal scales	7	8.2	0.59	(7-9)
Fin element counts				
First dorsal	6	6.5	0.57	(5-7)
Second dorsal	9	8.1	0.55	(7-9)
Anal	10	9.8	0.67	(8-11)
Pectoral	11	10.7	0.48	(10-11)
Position of fins				
OD ₁ to TV	F 4	F 3.4	0.69	(1.5- 4.5)
OD ₁ to T Pec	B 2.5	B 3.4	0.74	(2.0- 5.0)
OV to T Pec	0	0	0.75	(B 1- F 2)
Other values				
Gill rakers in 1st lower gill arch	15	15.7	0.79	(14-17)
Position of anus to TV	F 1.5	F 1.5	0.56	(0.5- 3.0)

fin is recorded as a number of scales behind the vertical through tips of pectorals and in front of tips of ventrals. The position of the origin of ventrals is recorded as the number of scales behind or in front of the vertical through pectoral tips. The mid-lateral scale count is always taken as the number of scales from the dorsal origin of the pectoral fin to the hypural joint. All measurements were made with calipers and were read to the nearest 0.1 mm.

Morphometric measurements and meristic counts have been recorded for thirty specimens (holotype and paratypes) (Table 1). The general description is based on characters of the holotype, 29 paratypes, and to some extent an additional 77 specimens.

DESCRIPTION

Atherinosoma wallacei, n.sp.

Holotype, WAM — P. 27275-001, 41.2 mm SL, collected by beach seine 21 May 1980, type locality: Guildford, Swan-Avon River system, Western Australia, 31°54'S 115°59'E.

Paratypes — 29 specimens. WAM — P. 27276-001, (4 specimens), 44.8-47.3 mm SL, 21 May 1980, Guildford. WAM — P. 27277-001, (3), 41.8-54.1 mm SL, 6 November 1980, mouth of Murray River, 32°35'S 115°57'E. WAM — P. 27278-001, (2) 43.2 and 44.0 mm SL, 31 October 1980, Shelley Basin, Canning River, 32°00'S 115°53'E.

AMS — I. 22527-001, (5), 37.5-45.2 mm SL, 21 May 1980, Guildford. BMNH, 1981.11.30.20.22 (3), 47.7-53.5 mm SL, 18 December 1980, Canning River, 32°02'S 115°53'E.

MNHN, 1981-1259 (3), 40.2-43.2 mm SL, 17 October 1979, Guildford.

USNM — 228884, (3), 39.3-43.6 mm SL, 17 October 1979, Guildford.

UMMZ — 209402, (1), 30.7 mm SL, 17 October 1979, Guildford.

UMMZ — 209404, (1), 37.4 mm SL, mouth of Murray River, Western Australia.

UMMZ — 209403, (1), 43.9 mm SL, Shelley Basin, Canning River.

CAS — 48752, (3), 34.5-40.2 mm SL, 17 October 1979, Guildford.

Museum abbreviations, WAM = Western Australian Museum, AMS = Australian Museum Sydney, BMNH = British Museum of Natural History, MNHN = Muséum National D'Histoire Naturelle, USNM = United States National Museum, UMMZ = University of Michigan Museum of Zoology, CAS = California Academy of Sciences.

MORPHOMETRICS (range and mean values)

Head in SL 3.6-4.8 (4.2); greatest body depth in SL 5.5-7.9 (6.6); inter-orbital in head 3.4-4.3 (3.9); snout in eye 0.9-3.0 (1.6); premaxilla in eye 0.8-1.4 (1.1); height of premaxillary process in eye 1.4-2.4 (2.0); least depth

of caudal peduncle in SL 10.4-17.0 (15.2); distance from origin of snout to origin of ventrals 2.2-2.7 (2.4) in SL.

MERISTICS (range and mean values)

Midlateral scales 36-45 (39.4); transverse scales 5-6 (5.3); predorsal scales 12-17 (14.5); interdorsal scales 7-11 (8.6); dorsal fins V-VIII, I,i,7-9; anal I,i,8-11; pectoral I,i,9-13. Gill rakers in first lower gill arch 14-17 (15.7). Vertebrae 38-41 (39.5).

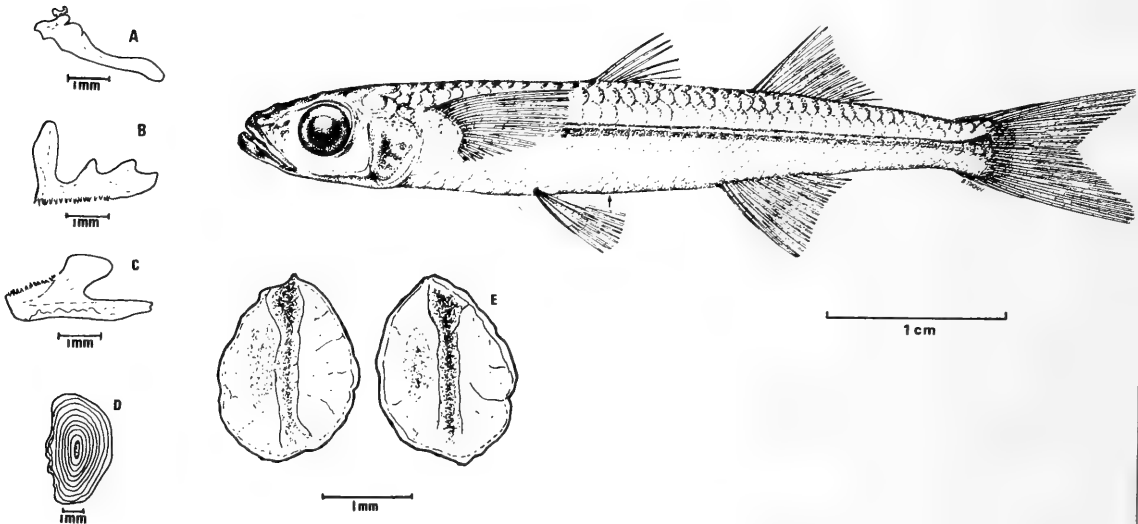


Fig. 1. Holotype of *Atherinosoma wallacei*. (a) Premaxilla, (b) maxilla, (c) dentary and (d) lateral body scales are drawn from an alizarin preparation of an unregistered specimen at different magnifications as indicated. Otoliths (e), medial view with anterior end pointing upwards in diagram.

Origin of first dorsal 1.5-4.5 scales in front of vertical through tips of ventrals and 2-5 scales behind vertical through tips of pectorals. Origin of ventrals from 2 scales in front to 1 scale behind vertical through tips of pectorals. The characters in this paragraph are based only on the holotype and paratypes.

Small slender, subcylindrical species. Mouth moderately small, with posterior end of maxilla reaching a point approximately below anterior margin of orbit. Upper jaw protrusible, but not to the same extent as in many other atherinids. Labial ligament not restricting gape of mouth. Lateral process of premaxilla small

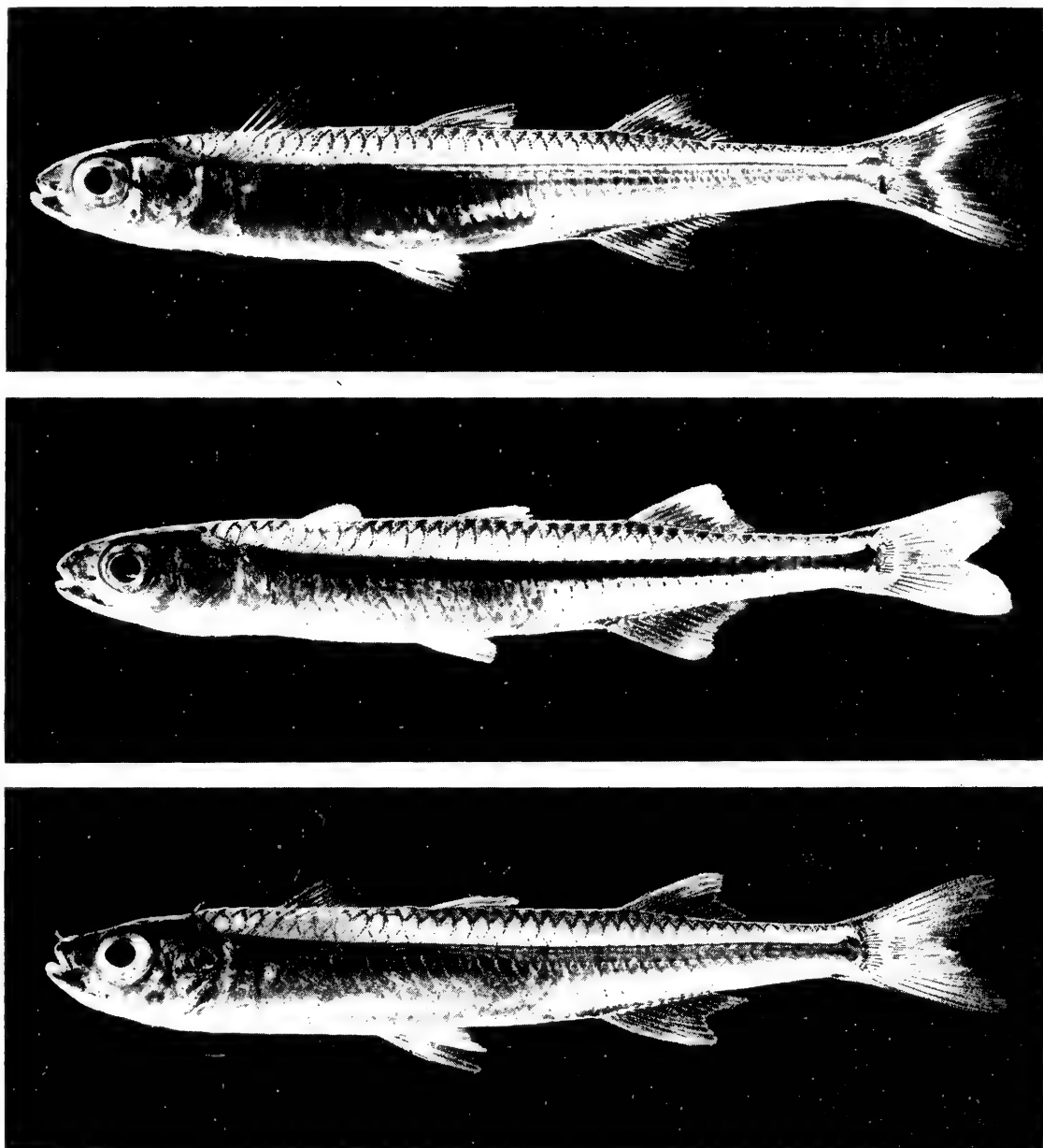


Fig. 2. Photograph of *Atherinosoma presbyteroides* (top), *Atherinosoma elongata* (middle), and *Atherinosoma wallacei* (bottom), with total lengths of 48.9, 48.0 and 46.5 mm respectively.

but distinct, frequently hook shaped and with its apex pointing backwards. Free edge of premaxilla convex and lying obliquely to horizontal. Posterior rami of dentaries very highly elevated. Small teeth are present in upper and lower jaws. Teeth usually present on vomer and palatines and in some specimens on the tongue where they form round irregular patches. In smaller specimens, the teeth may be weakly developed or absent from some of the bones listed above. Body scales small, usually dorsoventrally oval, with circuli complete and distinct. Preopercle with 3-4 scales. Gill rakers slender; length equal to or slightly less than diameter of pupil. Anus always in front of tips of ventral fins. Swimbladder curves upwards and backwards and ends immediately above origin of anal fin.

Preserved specimens whitish, but dark or pigmented in certain regions. Thus, scales above mid-lateral band are outlined by melanophores and the mid-lateral band is black or copper coloured, particularly in recently preserved specimens. Ventral body surface unpigmented. Fins slightly dusky, bases usually darkly pigmented. Dorsum of head, snout and sides of dentary and maxilla dark. Operculum usually silvery or white but with dark dorsal pigmentation. Eye silvery or black. Back of live specimens olive green and bearing scales whose perimeters are etched with dark melanophores. A slight silvery sheen covers the abdomen. A sharply defined lateral bronze stripe runs from operculum to hypural. When viewed with transmitted light, the posterior portion of the swim bladder can be clearly distinguished from the gut mass as a translucent structure.

This species is named after J. Wallace whose cooperation and encouragement during this study of atherinids was invaluable.

DISCUSSION

SYSTEMATIC RELATIONSHIPS

Comparisons between the data given in Table 2 for the characters of *A. wallacei* and those obtained for other *Atherinosoma* species in south-western Australia, suggest that *A. wallacei* is more closely related to *A. presbyteroides* than to *A. elongata*. Since the hardyheads are essentially a marine group, it can be postulated that *A. wallacei* evolved from a stock similar to that representing *A. presbyteroides*. In this context, it is of interest that our current study shows that, at least in the Swan-Avon system, the population of *A. presbyteroides* is found primarily in the lower estuary whereas *A. wallacei* is largely confined to the upper estuary and more inland areas of the river system. Since *A. elongata* largely occupies the middle estuary, the atherinid species tend to form a succession up the estuary from *A. presbyteroides* to *A. elongata* to *A. wallacei*. Fish collected in the Murray River, Peel Inlet and Harvey Estuary, together with an examination of WAM material, supports the view that *A. wallacei* tends to be more abundant in reduced salinities (Potter *et al.*, in prep.). Indeed, a survey of the records of atherinids in a number of south-western rivers shows that *A. wallacei* is the only *Atherinosoma* species consistently found in more inland areas of these systems

TABLE 2. Data on characters important in helping to separate the three species of *Atherinosoma* found in the Swan-Avon and Murray Rivers in south-western Australia.

	<i>A. wallacei</i>	<i>A. presbyteroides</i>	<i>A. elongata</i>
Midlateral scales			
\bar{x}	39.5	42.7	38.3
S.D.	1.6	1.1	1.4
Range	36-45	41-45	35-41
n	82	51	38
Gill rakers in lower gill arch			
\bar{x}	15.6	17.0	13.2
S.D.	1.4	0.8	0.7
Range	14-17	16-19	12-15
n	107	51	38
Largest gill raker in pupil			
\bar{x}	1.2	0.9	1.9
S.D.	0.1	0.1	0.3
Range	0.6-1.5	0.6-1.1	1.4-2.7
n	100	40	42
Rear end of upper jaw.	Extends to approximately the anterior margin of the eye.	Extends below anterior margin of the eye.	Never extends to anterior margin of the eye.
Appearance of swim bladder in fresh specimens viewed by transmitted light.	Posterior portion translucent and clearly distinct from gut mass. Rear end passes upwards and backwards.	Posterior portion opaque and not clearly distinct from gut mass. Rear end passes upwards and backwards.	Posterior portion opaque and not clearly distinct from gut mass. Rear end passes vertically upwards.

(Prince, *et al.*, in press). Moreover, it is evident that the succession formed through the Swan-Avon by the three *Atherinosoma* species is repeated in several different rivers. The significance of the marked tendency for atherinids to segregate in estuaries is discussed in detail in Prince, *et al.* (in press).

Two *Atherinosoma* species (and also very occasionally all three species) have been collected in the same sample. Under these circumstances, it was possible to separate the animals when live, freshly killed or frozen using a combination of the last two characters listed in Table 2. Thus, the presence of a short mouth and a swim bladder terminating in a right angle can be used to distinguish *A. elongata* from *A. presbyteroides* which has a much longer mouth and an upwards slanting end to the swim bladder. While the size of the mouth in *A. wallacei* tends to be intermediate between that of *A. elongata* and *A. presbyteroides*, this species is most clearly distinguished by the fact that the posterior portion of the swim bladder is translucent.

In considering the capture and subsequent identification of individuals, it is of value to record two additional observations pertaining to *A. presbyteroides* and *A. wallacei*. *A. presbyteroides* tends to be much more fragile and, unless treated with great care, it dies during capture or subsequent transportation to the laboratory. By contrast, *A. wallacei* (and also *A. elongata*) are so much more hardy that they can be used as experimental laboratory animals (McLaughlin, pers. comm.). Furthermore, even when *A. wallacei* and *A. presbyteroides* that had died during capture were brought back on ice, the flesh of the former species remained firm, whereas that of the latter species deteriorated rapidly and became soft. Since these differences are found in animals caught together, they reflect genuine interspecific physiological differences rather than environmentally induced differences.

While living, freshly killed or frozen individuals of the three *Atherinosoma* species can be relatively easily distinguished, identification is more difficult with formalin or alcohol-preserved specimens. However, it is usually possible to distinguish *A. elongata* using just the position of the rear end of the mouth relative to the eye and the relative size of the largest gill raker (Table 2). Although there are significant differences between *A. wallacei* and *A. presbyteroides* in the numbers of mid-lateral scales ($P < 0.01$) and gill rakers in the lower gill arch ($P < 0.01$), and also the relative size of the longest gill raker ($P < 0.01$), the ranges for each of these characters in these two species overlap. However, by considering each of these characters and the relative position of the rear end of the mouth, it is usually possible to distinguish the two species with certainty.

SOME FURTHER NOMENCLATURAL POINTS

The characteristic features of *A. presbyteroides*, *A. elongata* and *A. wallacei* given in this paper help to justify the use by Ivantsoff (1978) of certain species names for *Atherinosoma* spp. (see earlier section), and to clarify further the reasons for previous taxonomic problems.

A NEW SPECIES OF ESTUARINE AND INLAND WATER SILVERSIDE

Atherinids named *Atherinichthys edelensis* and *Atherinichthys obscurus* were described from the Swan by Castelnau in 1873 and 1876 respectively. Although the types of both of these atherinids are in poor condition, both Whitley (1943) and Ivantsoff (1978) concluded that the two species were synonyms. Castelnau (1873) recorded that in *A. edelensis* the "silvery" colour of the mid-lateral band is retained after preservation. Whitley (1943) stated that these type specimens came from Fremantle. Since the former feature is a characteristic of *A. presbyteroides*, and Fremantle is located in the lower estuary where *A. presbyteroides* is by far the most abundant *Atherinosoma* species, this provides further evidence that *edelensis* is likely to be a synonym of *presbyteroides*. Moreover, the counts for the mid-lateral scales and gill rakers, and also the description of the position of the eye recorded for the type of *edelensis* by Ivantsoff (1978), agree with those given in this paper for *A. presbyteroides* collected mainly from the lower Swan-Avon (Table 1). It should be noted, however, that the atherinid shown in Fig. 2 of Whitley (1955) and designated as *Atherinosoma edelensis* from an inland region (Northam) of the Swan-Avon is *Atherinosoma wallacei* and not *A. presbyteroides*. The point to remember here is that these two species are morphologically very similar and that it was not until the description of *A. wallacei* in the present paper that it was recognised that *A. presbyteroides* was found only in the lower part of the Swan-Avon.

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The Fish Fauna of Brackish Water Prawn Farming Ponds at Port Stephens, New South Wales

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ABSTRACT

A diverse fish fauna (49 species) was recorded in four tidal 0.11 ha prawn farming ponds which appear to act as fish traps. The potential deleterious effects of twelve of these species on prawn growth or survival are discussed in terms of the diet and reproductive biology of these fishes. Tarwhine (*Rhabdosargus sarba*) may be the most serious competitors with prawns for food while short- and long-finned eels (*Anguilla australis* and *A. reinhardtii*) are probably the greatest threat as predators especially as larger individuals appear to bypass the screens which act as filters during tidal water exchange.

INTRODUCTION

Two experimental prawn farming projects are being undertaken in ponds at Port Stephens, New South Wales. In the first project, juvenile school prawns (*Metapenaeus macleayi*) are collected from the Clarence River, N.S.W. and grown for up to three months to improve their market value (Maguire, 1976, 1980a, b; McBride and Maguire, 1979). In the second project, artificially reared postlarval prawns (*Penaeus plebejus*, *P. esculentus* or *Metapenaeus bennettiae*) are grown for 6-9 months from mid-spring onwards (Maguire, 1976).

The presence of certain fishes within prawn farming ponds is undesirable because they prey upon prawns or compete for their food (Maguire, 1980a). Fish within the ponds can be killed by draining or poisoning ponds shortly before stocking with prawns but fish may continue to enter the ponds during the farming period. In the second of the above prawn farming projects, these fish may remain in the ponds long enough to grow to a size at which they could prey upon the prawns prior to harvest. This is unlikely to be a problem in the first project which involves shorter farming periods but the fish could still compete with the prawns for food.

The aims of the present study are to describe the composition of the fish fauna within the ponds and to relate this information to their feeding habits

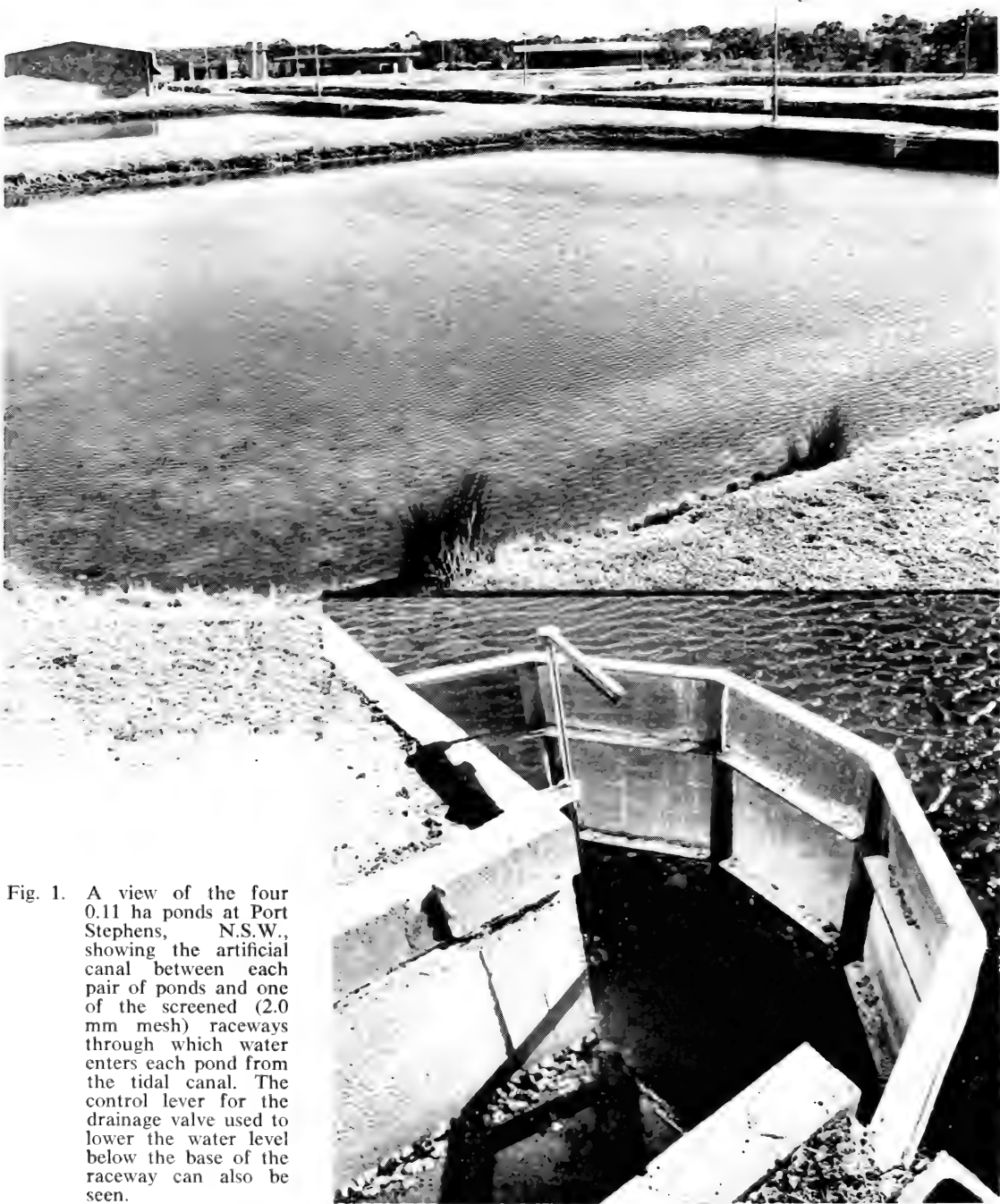


Fig. 1. A view of the four 0.11 ha ponds at Port Stephens, N.S.W., showing the artificial canal between each pair of ponds and one of the screened (2.0 mm mesh) raceways through which water enters each pond from the tidal canal. The control lever for the drainage valve used to lower the water level below the base of the raceway can also be seen.

and reproductive biology. This should enable fishes which are likely to seriously affect prawns stocked into the ponds, especially by preying upon them, to be identified. The present study complements that of Maguire and Bell (1981) in which competitive relationships between school prawns and some of the more common fishes in the ponds were investigated in experimental enclosures (pens) within the ponds.

MATERIALS AND METHODS

DESCRIPTION OF PONDS

The four 0.11 ha prawn farming ponds used in this study are located at the Brackish Water Fish Culture Research Station, Port Stephens, N.S.W. ($32^{\circ}42'S$, $152^{\circ}12'E$). These square ponds were excavated in an area of *Sporobolus virginicus* saltmarsh, the seaward fringe of which is occupied by *Avicennia marina* and *Aegiceras corniculatum* mangroves. The walls of some of the ponds and the adjacent tidal canal (Fig. 1) are being slowly colonised by these mangroves. The pond bottoms contain large amounts of wood and leaf detritus and fine-medium grade sand (125-500 μm grain size).

Water from an artificial canal connecting with the Port Stephens estuary enters each pond through a 2.0 mm mesh stainless steel screen after passing along a 0.9 m wide concrete raceway, the base of which is at a tidal level of 1.4 m above Indian Spring Low Water (Fig. 1). In each pond the average daily tidal water exchange (through 2.0 mm steel mesh screens) is approximately 70% of pond volume unless restricted during farming trials. Unless the drainage valve installed within the screened end of each raceway is opened, water is retained to at least raceway base level so that each pond contains approximately 1 m of water at low tide. The maximum water level recorded in the ponds is 2.3 m above Indian Spring low water; resulting in a maximum water depth of 1.9 m within the ponds.

TEMPERATURE AND SALINITY MEASUREMENTS

Pond bottom water temperature and salinity measurements were taken daily in whichever pond received unrestricted tidal ventilation. Temperature recordings were made using thermographs or maximum-minimum thermometers. Salinity readings were taken with a Yeokal model 602, Hamon-type, salinity-temperature meter.

FISH CENSUS

In January 1978 one pond was drained to a depth of 20 cm and poisoned by spraying with 2L of a rotenone solution (2.6% active ingredient) which killed all fish within the pond. Prior to the census the pond had not been stocked with prawns, netted or poisoned for 18 months and had usually received an

unrestricted rate of water exchange. An exhaustive collection of fishes was made with dipnets both within the pond and from the pond edge. The number of individuals of each species, their total weight and length range were then determined.

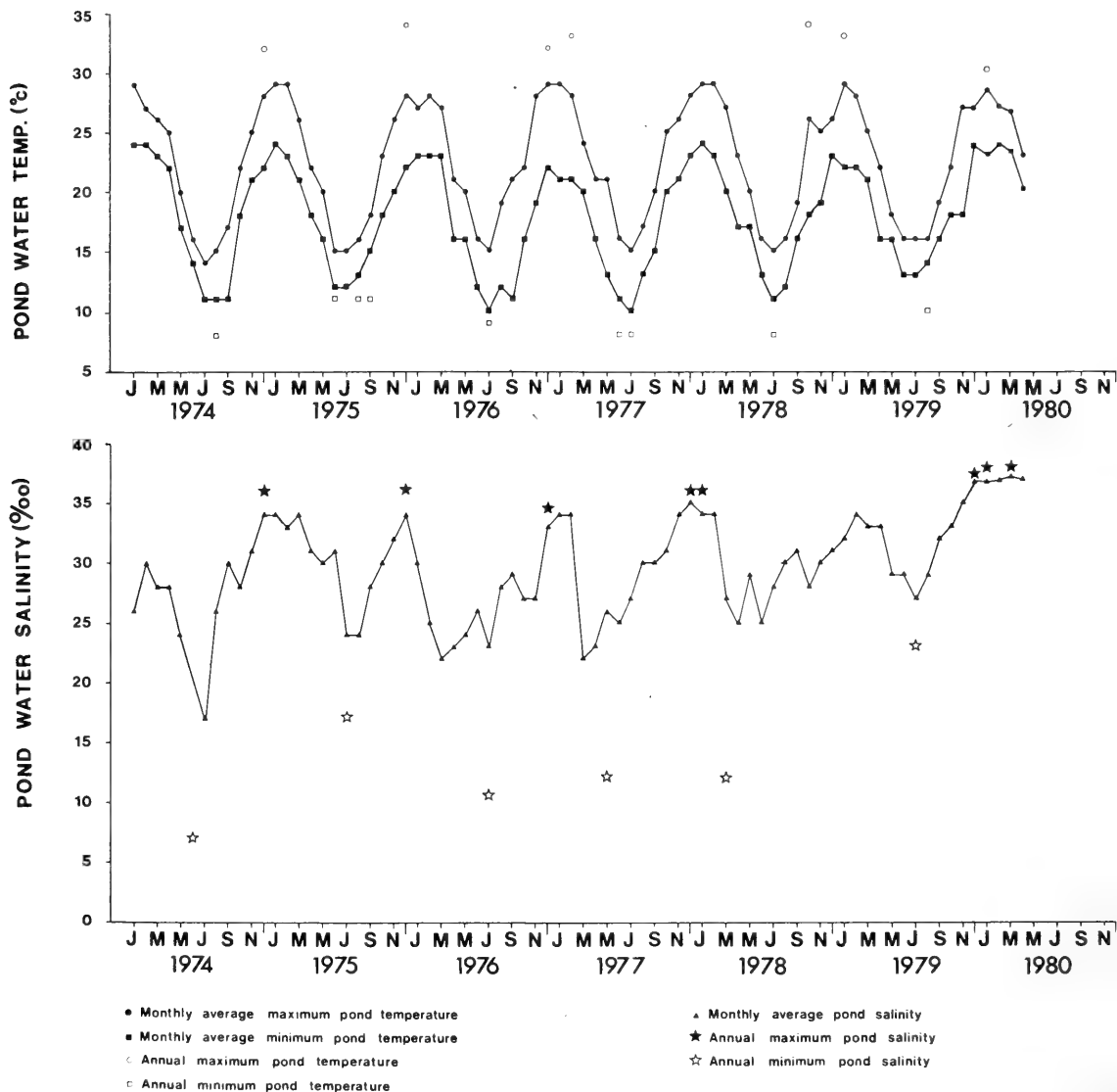


Fig. 2. Average monthly and annual extreme temperature and salinity values based on daily readings taken near the bottom of a 0.11 ha pond receiving unrestricted water exchange at Port Stephens, N.S.W.

RESULTS

Monthly averages of daily salinity and maximum and minimum pond water temperature readings in ponds receiving unrestricted water exchange during 1974-1980 are shown in Fig. 2. The extreme pond temperature and salinity ranges during this period were 8-34°C and 7-38‰ respectively.

TABLE 1. Fish species collected by poisoning a 0.11 ha prawn farming pond at Port Stephens, New South Wales.

Fish species	Common name	No. caught	Total wt. (g)	Length range (mm)
Anguillidae				
<i>Anguilla australis</i>	Short-finned eel	4	256.7	195-450 ^a
<i>Anguilla reinhardtii</i>	Long-finned eel	5	500.0	120-500 ^a
<i>Anguilla</i> spp	Juvenile eels	170	162.8	80-165 ^a
Ophichthyidae				
<i>Ophisurus serpens</i>	Serpent eel	5	163.7	240-610 ^a
Hemirhamphidae				
<i>Hyporhamphus australis</i>	Sea garfish	8	79.4	85-195 ^b
Atherinidae				
<i>Pseudomugil signifer</i>	Southern blue-eye	10	1.0	15-30 ^b
<i>Atherinosoma microstoma</i>	Hardyhead	1	0.3	35 ^b
Scorpaenidae				
<i>Centropogon australis</i>	Fortescue	26	35.2	23-65 ^a
Centropomidae				
<i>Velambassis jacksoniensis</i>	Glass perch	111	190.6	30-50 ^b
Theraponidae				
<i>Pelates sexlineatus</i>	Six-lined trumpeter	11	151.3	85-110 ^b
Sillaginidae				
<i>Sillago ciliata</i>	Sand whiting	2	4.5	60-65 ^b
Gerridae				
<i>Gerres ovatus</i>	Silver-biddy	57	982.5	25-115 ^b
Sparidae				
<i>Rhabdosargus sarba</i>	Tarwhine	526	1565.0	45-131 ^b
<i>Acanthopagrus australis</i>	Yellowfin bream	152	1055.0	40-205 ^b
Monodactylidae				
<i>Monodactylus argenteus</i>	Batfish	1	5.4	65 ^b
Girellidae				
<i>Girella cyanea</i>	Bluefish	20	47.5	35-65 ^b
Mugilidae				
<i>Mugil cephalus</i>	Sea mullet	2160	26115.0	65-250 ^b
<i>Myxus elongatus</i>	Sand mullet	360	720.0	30-60 ^b
plus <i>Liza argentea</i>	Tiger mullet			
Blenniidae				
<i>Omobranchus anolius</i>	Sabre-toothed oyster blenny	4	5.8	50-64 ^a
<i>Omobranchus rotundiceps</i>	Sabre-toothed oyster blenny	1	1.1	54 ^a

TABLE 1 Continued

Fish species	Common name	No. caught	Total wt. (g)	Length range (mm)
Gobiidae				
<i>Gobiopterus semivestita</i>	Transparent goby	185 ^c	1.4	14-19 ^a
<i>Pseudogobius olorum</i>	Swan River goby	162	81.0	13-39 ^a
<i>Cryptocentroides cristatus</i>	Crested goby	5	7.3	50-63 ^a
<i>Mugilogobius stigmaticus</i>	—	12	12.2	31-55 ^a
<i>Mugilogobius paludis</i>	—	4	1.2	28-34 ^a
<i>Favonigobius exquisitus</i>	—	91	79.9	15-66 ^a
<i>Favonigobius lateralis</i>	—	24	31.9	37-67 ^a
<i>Favonigobius tamarensis</i>	Tamar River goby	23	11.3	15-53 ^a
<i>Acentrogobius</i> sp.	—	55	147.1	23-72 ^a
<i>Arenigobius</i> sp.	—	5	5.8	43-48 ^a
<i>Arenigobius frenatus</i>	—	58	211.4	26-105 ^a
<i>Redigobius macrostomus</i>	Largemouth goby	23	8.4	23-40 ^a
Eleotridae				
<i>Philypnodon grandiceps</i>	Flathead gudgeon	7	9.9	47-61 ^a
<i>Gobiomorphus australis</i>	Striped gudgeon	1	1.0	40 ^a
Bothidae				
<i>Pseudorhombus jenynsii</i>	Small-toothed flounder	1	26.0	101 ^a
Soleidae				
<i>Achlyopa nigra</i>	Black sole	3	103.3	100-175 ^a
Monacanthidae				
<i>Meuschenia trachylepis</i>	Yellow-finned leather jacket	1	6.6	75 ^a
Tetraodontidae				
<i>Torquigener hamiltoni</i>	Hamilton's toadfish	29	434.0	25-120 ^a
TOTAL (38 species)		4323	33222.6	13-610

a Total length (T.L.); b Length to caudal fork (L.C.F.); c A large number of very small (<0.01 g average body weight) transparent gobies remained uncounted in the pond.

TABLE 2. Additional fish species recorded from prawn farming ponds at Port Stephens, New South Wales.

Family	Fish species	Common name
Engraulidae	<i>Engraulis australis</i>	Anchovy
Hemirhamphidae	<i>Hyporhamphus ardelio</i>	River garfish
Belonidae	<i>Strongylura leiura</i>	Long-tom
Syngnathidae	<i>Hippocampus whitei</i>	Seahorse
Platycephalidae	<i>Platycephalus fuscus</i>	Dusky flathead
Girellidae	<i>Girella tricuspidata</i>	Blackfish
Callionymidae	<i>Callionymus calcaratus</i>	Stinkfish
Gobiidae	<i>Bathygobius krefftii</i>	Krefft's goby
	<i>Nesogobius pulchellus</i>	Pretty goby
Eleotridae	<i>Hypseleotris compressus</i>	Emperor gudgeon
Monacanthidae	<i>Monacanthus chinensis</i>	Fan-bellied leatherjacket
TOTAL (11 species).		

FISH FAUNA OF BRACKISH WATER PRAWN FARMING PONDS AT PORT STEPHENS

The abundance and biomass of the 38 fish species belonging to 32 genera and 20 families) recorded during the census of a 0.11 ha pond are given in Table 1. Eleven species of fish (9 and 5 additional genera and families, respectively) not collected during the census but recorded at other times from the ponds are noted in Table 2. The most abundant fish caught during the census was sea mullet (*Mugil cephalus*) which accounted for 78.6% of the total fish biomass and 50.0% of the total number of individual fish collected. Other relatively abundant fishes included short- and long-finned eels (*Anguilla australis* and *A. reinhardtii*), glass perch (*Velambassis jacksoniensis*), silver-biddies (*Gerres ovatus*), tarwhine (*Rhabdosargus sarba*), yellowfin bream (*Acanthopagrus australis*), sand and tiger mullet (*Myxus elongatus* and *Liza argentea*) and several species of Gobiidae. These fishes were often abundant on other occasions when the ponds were harvested or poisoned prior to being stocked with prawns. Six species were considered to be potential predators of juvenile penaeid prawns within the ponds on the basis of studies of the stomach contents of fishes in N.S.W. estuaries (Table 3).

TABLE 3. Potential fish predators of prawns (> 2.5 g body weight) in prawn farming ponds at Port Stephens, New South Wales.

Fish species	Common name
<i>Anguilla australis</i> ^{ad}	Short-finned eel
<i>Anguilla reinhardtii</i> ^{ae}	Long-finned eel
<i>Platycephalus fuscus</i> ^{bcef}	Dusky flathead
<i>Sillago ciliata</i> ^{bdf}	Sand whiting
<i>Acanthopagrus australis</i> ^{acef}	Yellowfin bream
<i>Pseudorhombus jenynsii</i> ^{bc}	Small-toothed flounder

a Common in ponds.

b Only found in small numbers in ponds.

c Prawns found to be a major food item for this species (Thomson, 1959).

d Prawns found to be a minor food item for this species (Thomson, 1959).

e Prawns found in the stomachs of this species (Glaister, 1977).

f Prawns found in the stomachs of this species in Botany Bay, N.S.W. (Bell, 1980).

DISCUSSION

The water temperatures in these shallow ponds fluctuated more than those recorded by Wolf and Collins (1979) at the surface of the Port Stephens estuary near the artificial canal leading to the ponds. The annual minimum and maximum salinities were usually higher in the ponds than at Wolf and Collins' estuarine station. These large fluctuations in water temperature and salinity have not prevented the establishment of a large and diverse fish community in the prawn farming ponds. This can be seen in the comparison of the results of the census (Table 1) and those of the State Pollution Control Commission (S.P.C.C., 1981a).

They recorded a maximum of only 25 fish species and 2997 individual fish in any bimonthly sample taken over two years by poisoning a similar area of mangrove creek in Botany Bay, N.S.W.

Prawn farming ponds in other countries have also been found to contain diverse fish communities (Hall, 1962; Terazaki *et al.*, 1980). The composition of the diverse fish community in the Port Stephens ponds is probably related to the mesh size of the pond screens. All estuarine water and fish (except *Anguilla* spp.) entering or leaving the Port Stephens ponds have to pass through these screens which prevent fish longer than 10 mm (depending on shape) from entering or leaving the ponds. Thus many of the fish which entered the pond as eggs, postlarvae or small juveniles in the 18 months preceding this study would have been trapped in the ponds and recorded in the census. It is likely that the amount of tidal water exchange has a major effect on the number of individual fish inhabiting the ponds.

The ponds were not only characterised by their large fish community but also by the dominance within this community, in terms of biomass, of *Mugil cephalus*. Parker *et al.* (1972) also noted that this species was abundant in prawn farming ponds and Tang (1961), Silva *et al.* (1977) and Terazaki *et al.* (1980) suggested that various species of *Mugil* compete for food with prawns in ponds. However Maguire and Bell (1981) demonstrated that juvenile *Mugil cephalus* 55-155 mm (total length) had no apparent effect on the growth or survival rates of school prawns in pens within a pond even when stocked at high densities (1.5-7.6 fish/m²). In contrast tarwhine and yellowfin bream were found to compete for food with, and depress the growth rates of, school prawns in pens. Furthermore they showed that relatively small yellowfin bream, e.g., 90 mm LCF, prey upon juvenile school prawns in pens. Both of these species of fish are common in the Port Stephens ponds. The studies by Munro (1945), Bell (1980) and S.P.C.C. (1981b) suggest that small postlarval tarwhine, e.g., 5-15 mm long, are present in New South Wales estuaries in spring, i.e. when postlarval prawns are stocked into ponds. Thus when tarwhine enter ponds they could grow to a size at which they would seriously compete for food with prawns. Yellowfin bream have generally been found to reproduce in winter in New South Wales and southern Queensland (Munro, 1945; Dredge, 1976; Bell, 1980; S.P.C.C., 1981b). Thus many postlarval yellowfin bream may be too large to enter through the screens after the ponds have been poisoned and stocked with postlarval prawns in mid-spring.

Maguire and Bell (1981) concluded that several of the remaining common species of fish in the ponds had little effect on school prawn growth and survival. Thus the presence of tiger mullet, silver-biddies and transparent gobies may not be harmful in prawn farming ponds. However, there are several other species which were abundant, or potential predators, within the ponds but which were not studied by Maguire and Bell (1981). Short- and long-finned eels have been

considered to be potential predators of juvenile prawns (Table 3). Although the elvers of these species may be present in estuaries in temperate Australian regions for most of the year (Beumer, 1979 and personal communication, 1981) they may be too large to pass through the screens. However, elvers have been observed climbing the high vertical surfaces of dam walls in coastal New South Wales rivers (Bishop and Bell, 1978). It is also likely that juvenile and larger eels could bypass the screens and climb directly over the sloping pond walls. Hence *Anguilla* spp. may pose a serious threat as predators within the ponds. Shigueno (1975) found that *Anguilla japonica* could bypass screens and prey upon prawns in Japanese farming ponds.

Dusky flathead (*Platycephalus fuscus*), sand whiting (*Sillago ciliata*) and small-toothed flounder (*Pseudorhombus jenynsii*) reproduce in summer in New South Wales (Bell, 1980; S.P.C.C., 1981b) and would enter the ponds too late in the growing season to grow to a size at which they could be serious predators by the time the ponds are harvested. One fish which was common in the ponds but not studied by Maguire and Bell (1981) because of its susceptibility to handling was the glass perch (*Velambassis jacksoniensis*). However, this species feeds on plankton (Thomson, 1959) and should have little effect on the benthic prawns farmed in the ponds.

In conclusion it is apparent that a wide variety of fishes enter and survive in tidally flushed prawn farming ponds. In longer prawn farming operations involving the stocking of postlarval prawns, the potential exists for fish to grow large enough to be serious predators as well as competitors for food with prawns. It should be noted that the prawns also grow during the farming period but this increase in size does not necessarily prevent predation. Shigueno (1975) found that predation by fish was the major cause of mortality in Japanese prawn farming ponds despite the eradication of fish within the ponds prior to the stocking of postlarval prawns. However, the stocking of postlarval prawns in mid-spring could reduce the deleterious effects of some of these fishes. Should certain species enter the ponds sufficiently early in the farming period to seriously reduce prawn harvests, additional management measures may have to be adopted, e.g., the use of eel barriers, filtering of incoming water through finer screens or periodic removal of fish from ponds. A low water exchange rate would restrict the opportunities for fish to enter ponds but could also adversely affect the physico-chemical characteristics of the ponds (Maguire, 1980a).

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Reproduction and early stages of development in two species of Australian rainbowfishes, *Melanotaenia nigrans* (Richardson) and *Melanotaenia splendida inornata* (Castelnau).

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ABSTRACT

Reproductive behaviour, colouration of adult fish and development to hatching of *Melanotaenia nigrans* and *Melanotaenia splendida inornata* were studied under laboratory conditions during summer and autumn (February to early May). At $26^{\circ}\text{C} \pm 1^{\circ}\text{C}$, all observed pairs of fish spawned each day during this period. The eggs of the two species differed in size as well as in the number and colour of oil droplets. The rate of embryonic development under identical conditions of temperature and light was found to be almost parallel in the two species. However, the melanophore pattern of the developing embryos was found to be sufficiently different to identify each species. At hatching, the larvae were well developed, with functional mouth and well formed pectoral fins.

INTRODUCTION

Melanotaenia nigrans (Richardson, 1843), the black striped rainbowfish and *Melanotaenia splendida inornata* (Castelnau, 1875), the checkered rainbowfish, belong to the family Melanotaeniidae, a group of freshwater fishes endemic to Australia, New Guinea and the Aru Islands.

Although most species of melanotaeniids have been kept and bred in captivity since the early part of this century, little is known of their life history or their biology. Sterba (1963), Breder and Rosen (1966), Axelrod *et al.* (1971), Lake (1978) and Munro (1980) give brief notes on reproduction of some melanotaeniids whilst Beumer (1979), has published a short account of spawning behaviour, incubation period and size of prolarvae at hatching for *Nematocentris splendida* (= *Melanotaenia splendida splendida*, see Allen, 1980). K. A. Bishop (pers. comm.), who has studied the ecology of fish of the Alligator Rivers region, suggests that melanotaeniids in that region may either spawn daily for a period of about four to five months, or may spawn opportunistically if conditions are favourable. Beumer's findings (1979) confirm this view for the species of rainbows he studied in northern Queensland. Factors initiating reproductive behaviour in

rainbowfishes are not known but Beumer (1979) does suggest day-length could be a factor which may induce spawning.

Colour variability in melanotaeniids has been a source of confusion to students studying their life history and to taxonomists alike. Colour appears to vary from population to population of the same species as well as within a population, particularly during different stages of the fishes' life. Most of the rainbowfishes are also sexually dichromatic and this adds further difficulty to species recognition. Lake (1978) has recorded some of this variability in relation to age, sex, stress, habitat and during spawning. Munro (1980) has also given a description of several colour phases for two species of melanotaeniids from the south-eastern coast of Australia. The most recent of many references to spawning in rainbowfishes (Lake, 1971, 1978; Munro, 1958, 1967, 1980; and Beumer, 1979) record some aspects of sexual display but embryonic development and larval and juvenile growth are not discussed.

MATERIALS AND METHODS

Adult fish in breeding condition were collected in Northern Territory in late spring, between 17-20 November, 1980. Specimens of *M. nigrans* were taken from a small permanent water-hole at Koongarra (12°36'S 132°52'E) approximately 40 km south-east of Mudginbarry. *M. s. inornata* was collected in Ja Ja Lagoon, (12°32'S 132°53'E) about 10 km north of Mudginbarry Homestead. The fish were air freighted to Sydney, 3 to 4 fish to one small plastic bag containing about 400 mls of well oxygenated water. On arrival at Macquarie University, the fish were transferred to 200 litre tanks in which the water had been allowed to stand for one week.

Small amounts of frozen brine shrimp were fed to the fish on the day of arrival and dried commercial food (TetraMin brand) was given on the following day. A regime of three feeds a day was established (dry food twice a day and frozen brine shrimp once a day) as soon as the fish began accepting food. After three months, breeding pairs were selected and moved into separate 30 litre tanks containing fine leafed weed e.g. *Cabomba* sp. The temperature of the tanks was maintained at $26^{\circ} \pm 1^{\circ}\text{C}$.

The breeding tanks were cleaned every two to three weeks. Untreated tap water was found to be quite satisfactory whenever addition or change of water was necessary. Fungal infection, when it occurred, was treated by placing the fish in a separate 30 litre tank in which 7 drops of 1% Methylene Blue had been added to the water. The fish were subjected to this treatment for up to two weeks.

Fish spawned amongst weed and the eggs were removed as soon as possible to another 30 litre tank to prevent predation by adults. On hatching, the fry were fed Liquifry No. 1 and TetraMin Baby Fish Food "E" five times a day. From

the end of the second week brine shrimp nauplii were also given to the developing young to supplement their diet.

Eggs removed for study were transferred to 90 mm diameter covered plastic petri dishes in which a drop of 0.5% Malachite Green solution had been added to the water to minimize fungal infection. The petri dishes were moved to a thermally insulated room where the temperature was kept constant at $25^{\circ} \pm 1^{\circ}\text{C}$ and the photo-period maintained at 12 hours daylight per 24 hours throughout the period of incubation.

The behaviour, colour changes and spawning were observed and recorded for each pair of adult fish of both species. For convenience, the observed embryonic development was recorded in 24 stages, selected to point out and highlight some of the changes taking place. All measurements were made using an Olympus dissecting microscope with a graticule eye-piece. Heart rates of developing embryos were counted from first observed pulsations of the pericardial cavity up to the time of hatching.

RESULTS

COLOURATION AND BEHAVIOUR OF ADULT FISH DURING THE PRE-SPAWNING AND SPAWNING PERIOD

In aquarium conditions, pre-spawning behaviour usually occurs in the morning and may continue for up to an hour before spawning takes place. Initially the fish remain stationary, facing in the same direction, with their bodies apart but with the caudal fins touching, the caudal and pectoral fins fanning gently. During this period (5 to 10 minutes) the colours in both sexes become more intense but to a lesser extent in the female.

In *M. nigrans* males, the nape and pectoral fins become pale luminous orange, the dorsal fins bright yellow edged with black and the caudal, a deep sulphurous yellow. The anal and pelvic fins remain pale but are edged with red and black. The red colour extends along the body ventrally from the branchiostegals to one third of the way along the ventral edge of the caudal fin. The dark midlateral stripe which extends from the snout to the base of the caudal fin becomes prominent and a few red flecks appear on scales just below the stripe near the tail. Above the midlateral stripe, the body darkens from yellow-grey to very dark grey except for the area posterior to the dorsal fins where it becomes golden. Below the midlateral stripe, the body is iridescent mauve. In the female the colours are paler. The caudal fin is yellow and the midlateral stripe is prominent as in the male. The edges of the dorsal and anal fins are not coloured. In both sexes, a faint red spot is present on the operculum.

In *M. s. inornata* males, the edges of the fins and the checkering of the caudal and second dorsal fins become black. The nape may darken to black in

some but not all fish. The midlateral stripe is prominent, extending from the origin of the pectoral fin to the caudal peduncle. Near the tail, two shorter dark lines appear above and below the midlateral stripe. The normal orange-yellow longitudinal stripes become a more intense colour in both sexes. The males have an iridescent purple sheen in light. The operculum has a glowing red spot in both sexes. The pectorals do not become coloured in either males or females. In the females, the midlateral stripe darkens before spawning but the stripe is not as long as in males. The checkered appearance of the second dorsal fin becomes more noticeable and the colour of all the fins darkens except in the case of the pectorals.

Chasing follows immediately after the colour change. The males chase the females, swim below them and brush their vent area with erect dorsal fins or butt them in the vent region or in the area of the pectoral fins. The males frequently shake themselves as they swim below the females. They display erected fins as they swim beside or at right angles in front of the females. During the pre-spawning chasing and display, the males can become quite aggressive and nip the females if the latter do not show interest in the display. In the final phase of pre-spawning behaviour, the pair swim with their bodies parallel, sinking and rising and then remain in one place with heads touching and their bodies vibrating rapidly. After 3 to 5 seconds of this, eggs and milt are shed, the male swishes its tail and the eggs are seen swirling in the wake. Spawning usually occurs in the top 100 mm of the tank.

In aquarium conditions, spawning occurred daily during the summer months, almost always in the morning. However, if males and females in breeding condition, previously kept separately, are placed together, they may spawn late in the day. In such cases, preliminary pre-spawning behaviour may not occur.

TABLE 1. Comparison of biological data obtained from examination of eggs of *M. nigrans* and *M. s. inornata*.

	<i>M. nigrans</i>	<i>M. s. inornata</i>
Number of eggs examined	6	6
Egg diameter (mm)	1.05 (1.00-1.08)	0.88 (0.87-0.92)
Perivitelline space	0.05 (0.04-0.06)	0.05 (0.04-0.06)
No. oil droplets	45-55	55-65
Oil droplet diameters (mm)	0.02-0.07	0.01-0.08
Oil colour	Chartreuse	Golden
No. eggs per spawning	*50-70	*60-100

*Accurate counting of the eggs is difficult as the male disperses the eggs rapidly by the swishing of his tail. Also, many of the eggs are eaten before and after they attach to the weeds or other objects.

THE EGGS

The eggs of both species are similar, the major differences being in their size and in the number and colour of the oil droplets, (Table 1).

In both species studied, at spawning, the eggs are spherical and opaque with many filaments originating from one small area of the chorion. The filaments are straight and 20-30 mm in length. On coming into contact with a surface which is not smooth, such as weed, the filaments adhere and contract so that the eggs become suspended. The eggs, which become clear a few seconds after spawning, are large and have numerous small oil droplets at the pole where the filaments occur. The oil droplets appear to aid flotation of the eggs until they attach to an object by their filaments. The oil droplets move down the periphery of the egg to the opposite pole while the first four cleavages of the developing embryo take place.

The chorion is clear, smooth and colourless, and the yolk is also colourless and non-granular. The oil droplets do not coalesce, although they remain in the same position during the development of the embryo and diminish in number. Some are still apparent in the yolk sac just prior to hatching.

EMBRYOLOGY

The eggs of *M. nigrans* and *M. s. inornata* are telolecithal. Division is meroblastic and restricted to a small disc directly below the filaments. The yolk material remains undivided and is later covered by the periblast and enclosed by ectoderm.

Orderly movement of oil droplets towards the mid-polar periphery indicates that the eggs are fertilized. In unfertilized eggs, the oil droplets become randomly scattered within thirty minutes, and the yolk becomes a dense cloudy mass.

The general pattern of teleost embryo development is followed as discussed by Breder (1959), Armstrong and Child (1965), Llewellyn (1973, 1974) and Long and Ballard (1976). In the present study, the hatching prolarvae are more advanced embryonically than those studied by the above workers. At hatching the yolk sac is very reduced, the pectoral fins and mouth are present and functional and the prolarvae swim strongly. Feeding commences within 24 hours.

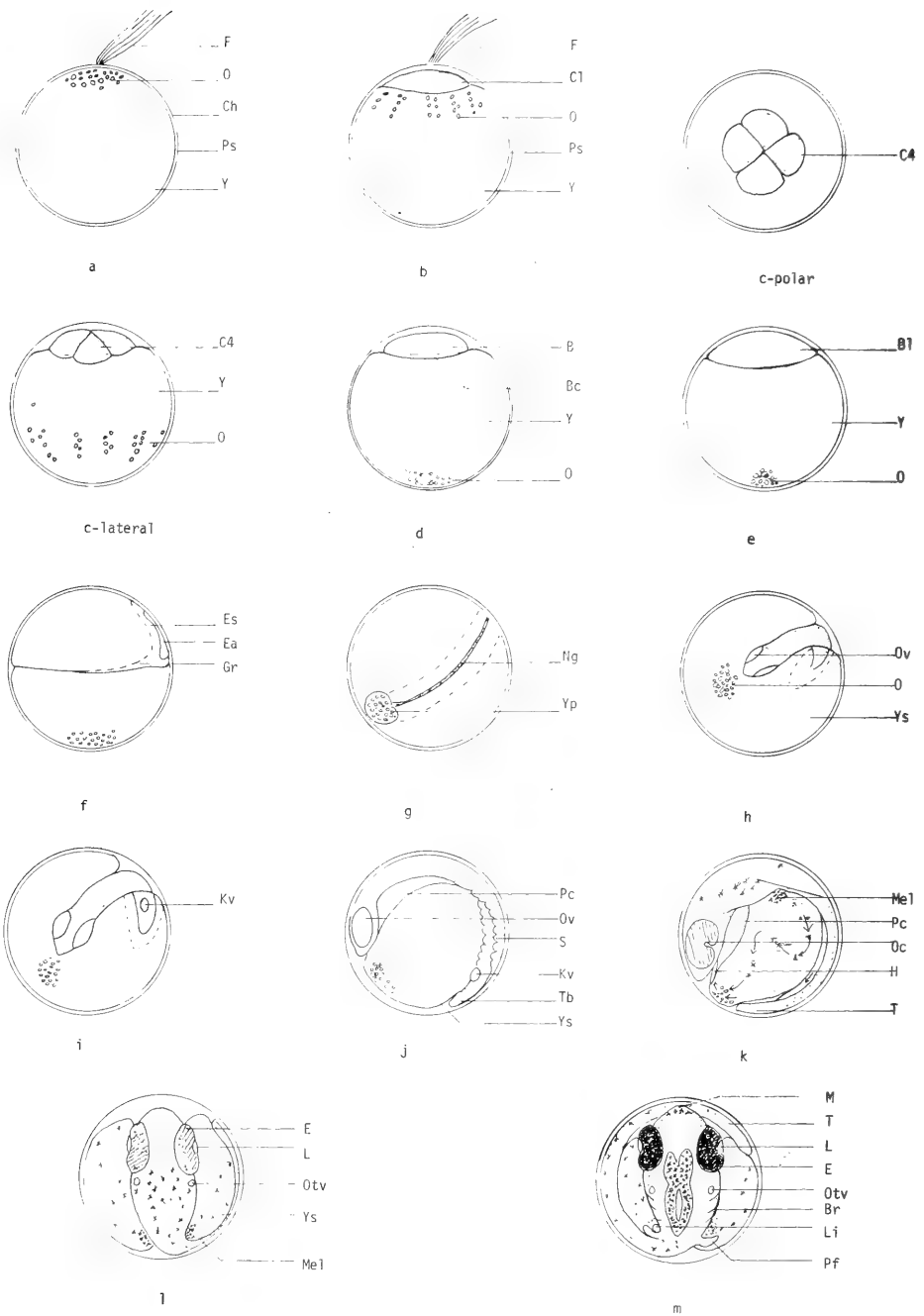
DESCRIPTION AND TIME OF STAGES DURING DEVELOPMENT OF EMBRYOS OF *M. nigrans* and *M. s. inornata*.

Temperature during development: $25^{\circ} \pm 1^{\circ}\text{C}$.

Photo-period: 12 hours light, every 24 hours.

Number of eggs examined for each species in this study: 6.

Times for later developmental stages are given to the nearest half hour.



RAINBOWFISHES, BREEDING AND EARLY DEVELOPMENT

STAGE	TIME	
	<i>M. nigrans</i>	<i>M. s. inornata</i>
1. Fertilized eggs. Oil droplets are directly below the filaments. (Fig. 1a).	0.5 s.	0.5 s.
2. First cell forms. Oil droplets show orderly movement towards the mid-polar periphery. (Fig. 1b).	0.66 h.	0.55 h.
3. Two cell stage. Oil droplets at mid-polar periphery of yolk.	1.5 h.	1.25 h.
4. Four cell stage. Oil droplets continue downward movement towards vegetal pole. (Fig. 1c).	2 h.	2 h.
5. Eight cell stage. Most oil droplets have reached the vegetal pole.	2.5 h.	2.5 h.
6. Sixteen to thirty two cells. Oil droplets are all at vegetal pole where they remain. They do not coalesce. (Fig. 1d).	3-4 h.	3-4 h.
7. Start of epiboly. Blastoderm flattens out and begins spreading downwards over yolk. (Fig. 1e).	5 h.	5 h.
8. Embryonic shield and germ ring visible. Blastoderm continues downward movement. (Fig. 1f).	14 h.	14 h.
9. Neural plate and groove visible. The yolk is now enclosed by the blastoderm except for the small yolk plug. (Fig. 1g).	20.5 h.	21.5 h.

Fig. 1. Embryonic development of *M. nigrans* and *M. s. inornata*. (a) Fertilized egg, 0.5 s; (b) First cell stage 0.55-0.66 h; (c) Polar and lateral view, four cell stage, oil droplets two thirds of the way to the vegetal pole, 2 h; (d) Blastodisc with blastocoele, 3-4 h; (e) Blastoderm flattening and beginning to spread downward over yolk, 5 h; (f) The germ ring, embryonic shield and axis are visible, 14 h; (g) Blastoderm covering yolk except for yolk plug, neural groove visible, 20.5-21.5 h; (h) Early embryo formed, optic vesicles apparent on head 23.5-24.5 h; (i) Optic vesicles have enlarged and Kupffer's vesicle is seen clearly, 26 h; (j) Caudal somites and pericardial cavity apparent, 27-27.5 h; (k) Heart appears in pericardial cavity. Flow of plasma is indicated by the arrows, 47-47.5 h; (l) Eye pigmented and lens formed, otic vesicles are visible, melanophores on head, tail and yolk sac. (Diagram shows melanophore pattern of *M. nigrans*), 54.5-55 h; (m) Mouth present edged with melanophores, yellow vesicle marks position of the liver, branchial arches apparent. (Diagram shows melanophore pattern of *M. s. inornata*, expanded by strong light), 98-100 h. B, blastodisc; Bc, blastocoele; Bl, blastoderm; Br, branchial arches; C1, one cell; C4, four cells; Ch, chorion; E, eye; Ea, embryonic axis; Es, embryonic shield; F, filaments; Gr, germ ring; H, heart; Kv, Kupffer's vesicle; L, lens; Li, liver; M, mouth; Mel, melanophores; Ng, neural groove; O, oil droplets; Oc, optic cup; Ov, optic vesicle; Otv, otic vesicle; Pc, pericardial cavity; Pf, pectoral fin; Ps, perivitelline space; S, somites; T, tail; Tb, tail bud; Y, yolk; Yp, yolk plug; Ys, yolk sac.

STAGE	TIME	
	<i>M. nigrans</i>	<i>M. s. inornata</i>
10. Optic vesicles apparent. Head of developing embryo is close to the oil droplets. (Fig. 1h.)	23.5 h.	24.5 h.
11. The optic vesicles are prominent features on the head. Kupffer's vesicle (Armstrong and Child, 1965; Ruck, 1980) is clearly visible. (Fig. 1i).	26 h.	26 h.
12. First caudal somites visible. The pericardial cavity is obvious below the head. (Fig. 1j).	27.5 h.	27 h.
13. Brain ventricles have enlarged. Optic cup is apparent, but no eye lens is visible.	30.5 h.	32 h.
14. First melanophores appear on the yolk sac.	38 h.	38.5 h.
15. Melanophores start to darken the optic cup and they also appear along the sides of the body and head.	47 h.	46.5 h.
16. Plasma, but no red blood cells, circulates through the heart and yolk sac vessels. The heart is a straight tube and the pulse rate can be measured from the movement of the pericardial cavity. The pulse is slow at first, but increases as the embryo develops. (Fig. 1k).	47.5 h.	47 h.
17. Flexing of the body and tail occurs. The tail extends free from the yolk sac. Embryo is two-thirds around yolk sac.	51.5 h.	49.5 h.
18. Otic vesicles visible. Red blood cells circulate through the heart and yolk sac vessels. Discontinuity of the blood flow through the heart indicates the boundary of the developing chambers. (Fig. 1l)	55 h.	54.5 h.
19. Pectoral fin buds appear as small semi-circular ridges. The eye lens is fully formed and retinal pigment is fairly dense. The swim bladder appears as a small vesicle just below junction of body and tail.	72 h.	72 h.

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STAGE	TIME	
	<i>M. nigrans</i>	<i>M. s. inornata</i>
20. Branchial arches are first seen. The yolk sac is reduced. The tail which moves frequently always comes to rest in the equatorial plane past the anterior part of the head.	96 h.	96.5 h.
21. The upper jaw is apparent, later edged by a row of melanophores. A yellow vesicle below and behind the left pectoral fin marks the position of the liver. The pectoral fins have grown and move freely. (Fig. 1m).	98 h.	100 h.
22. Meckel's cartilage can be seen as the lower jaw forms. Yellow colour spreads throughout the dorsal surface of the head.	102 h.	103 h.
23. The mouth opens and shuts frequently. Both upper and lower jaws are edged with melanophores. The heart chambers are well defined. The yellow colour has spread along the body and tail. The yolk sac is not visible when the embryo is viewed from the dorsal surface. Turning of the whole embryo within the chorion is frequent, particularly when the egg is subjected to strong light. Oil droplets are still present in the anterior of the yolk sac but are fewer in number.	128 h.	130 h.
24. Hatching. Prior to hatching the embryos lie with the tail coiled to one side rather than around the equatorial plane of the yolk sac. In <i>M. s. inornata</i> a spherical protuberance appears on the chorion directly in front of the mouth a few seconds before hatching.	155-159 h.	151-152 h.

The timing of the development of the embryos of the two species is almost parallel when conditions are constant, but the hatching of *M. s. inornata* occurs several hours earlier than in *M. nigrans*. The embryos are distinguishable by their melanophore pattern (Fig. 1l and 1m), although there is slight variability in

this pattern within each species. In both species, the size of the melanophores increases under strong light to produce continuous dark patches.

CHANGE IN RATE OF HEART BEAT DURING EMBRYONIC DEVELOPMENT

Rhythmic contractions of the pericardial cavity indicate the onset of circulation of plasma through the heart and yolk sac vessels. Red blood cells appear in the plasma seven to eight hours after the onset of circulation. The colour of the plasma becomes faintly pink, but gradually darkens to red as more red blood cells develop.

The pulsations of the pericardial cavity are initially slow, but increase in rate as the embryos develop. The correlation between increasing heart rate and age of embryo is $r = 0.852$ ($p < 0.001$) ($N = 39$) for *M. s. inornata* and for *M. nigrans*, $r = 0.841$ ($p < 0.001$) ($N = 38$).

DISCUSSION

In contrast to previous reports (Breder and Rosen, 1966; Lake, 1971; Beumer, 1979) it appears that melanotaeniids, specifically *M. nigrans* and *M. s. inornata* shed 50 to 100 eggs at each spawning. Survival of eggs is reduced by predation activity of the parents.

K. A. Bishop (pers. comm.) reports that melanotaeniids in the Alligator Rivers region may spawn only when conditions are favourable. Beumer (1979) suggests that *M. s. splendida* may spawn throughout the year. Following photo-period experiments, Beumer also indicated that day length could have been a factor which induced spawning. In this study both *M. nigrans* and *M. s. inornata* spawned every day during the summer months with a decline in spawning activity at the onset of autumn as day length shortened. Since the temperature was maintained at $26^{\circ} \pm 1^{\circ}\text{C}$, with food supply readily available, the photo-period could be regarded as a contributing factor to the decline in spawning activity. However, a number of fish maintained under a 12-hour light/dark cycle also stopped spawning, suggesting either an endogenous rhythm or that the female became totally spent after spawning daily for several months.

A wide pH range does not appear to affect reproduction of melanotaeniids. The water in which the fish were kept in our laboratory (pH 7.8) was more alkaline than that of their natural habitat (pH 3.9-6.7; K. A. Bishop, pers. comm.), yet the fish continued to thrive and spawn, and embryo development was normal.

Since *M. nigrans* and *M. s. inornata* can easily be kept and bred, they could be useful in laboratory experiments in which the relationships between reproduction and environmental requirements (such as photo-periodicity, temperature and pH) are studied.

RAINBOWFISHES, BREEDING AND EARLY DEVELOPMENT

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Macroinvertebrate Sampling Using a Dredge Net in a Farm Dam in Southwestern New South Wales

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ABSTRACT

The number of samples required to quantitatively sample the macroinvertebrates in 0.05 ha farm dam in southwestern New South Wales using a dredge net was investigated. Twenty samples, each from a 15 m x 0.46 m area of the dam floor, were collected. The numerically dominant species showed contagious distributions, and the distribution of the community was not influenced by wind or submerged terrestrial grass. In the dam studied, 8 samples would have given an estimate of the true mean number of macroinvertebrates per sample with 95 percent confidence limits and 40 percent accuracy.

INTRODUCTION

Farm dams are the most common lentic water bodies in Australia (Weatherley, 1967), and are comparatively simple ecosystems in which biological diversity may be low (Timms, 1980). Although such environments are favourable for quantitative study of species abundance, diversity and succession, little work has been conducted on the fauna of farm dams in Australia (Bayly and Williams, 1973). In a review of the ecology of farm dams, Timms (1980) concluded that for macroinvertebrates little more than species lists are available and that they are often difficult to interpret.

Several sampling methods have been employed in studying macroinvertebrates in farm dams. Croxford (1977) took sweep samples in open water, and entrapped animals associated with vegetation in a metal tube pushed vertically into the substrate. Walker (1974) used a sweep net in open water and among macrophytes, and a modified Macan-type sampler in vegetation growing from the dam edge into the water. A similar device was used by Weatherley and Nicholls (1955) for collecting epiphytic fauna. These authors were primarily interested in the qualitative aspects of their collections.

A small beam trawl used for collecting surface and bottom living animals was described by Ruello (1975). He gave a list of animals taken from inland waters of New South Wales, and reported that the beam trawl could be used for quantitative sampling of yabbies *Cherax destructor* in dams.

A sampling method which provides comparable data between sites and sampling times would enhance the value of data collected in studies on farm dams. Macan (1949) and Crisp (1962) showed that sweep nets were more satisfactory than hand grab-samplers or traps for sampling active free-swimming insects. A dredge net (Welch, 1948; Williams, 1980), which is similar to the beam trawl of Ruello (1975), operates on the same principle as a sweep net but allows a greater area to be sampled with less effort.

In the present study we used a dredge net to sample macroinvertebrates in a farm dam, in order to examine the distribution of individual taxa and the distributional homogeneity of community structure with respect to submerged grass and wind, and to determine the number of samples required to estimate the true mean with varying confidence intervals and degrees of precision.

MATERIALS AND METHODS

The dam was situated in southwestern New South Wales (34°56.2'S, 146°25.0'E). The geological origin of the area is Middle Ordovician, and the soils formed in the region are red earths (Northcote classification Gn2.11-3/2/15) (Crouch, 1974). The dam was rectangular, 26 m long, 19 m wide (surface area 0.05 ha) and 1.9 m at the deepest point. The walls had a 1:3 slope. The long axis of the dam was oriented east-west, and water runoff entered the dam from the eastern side. The substrate was clay, and suspended clay colloids caused the water to be very turbid (Secchi disc depth of 100 mm). The dam was devoid of vegetation, although seed-heads of the terrestrial "blown-grass" *Agrostis avenacea* had accumulated and submerged in the northeast corner. Sampling was conducted on 17 December 1979, between 1300 and 1500 hours, at which time the weather was fine and cloudy with a 12 to 18 knot wind from the northwest.

The dredge net (Fig. 1) was made of a 500 μ m mesh net. The open end was 460 mm x 310 mm, and the net tapered for 1 m to a collecting jar 60 mm in diameter. The net was supported 60 mm off the substrate by a frame attached to a ski on each side. A "kick chain" joined the two skis 170 mm in front of the mouth of the net.

A total of twenty samples, five from each side of the dam, was collected. For practical reasons, sampling was from the western, northern, eastern and southern banks respectively. The dredge net was released either from a boat or by wading out from the opposite bank from which it was being towed, and then towing it over 15 m of the dam floor at approximately 1 m/sec. The five tows from each bank were spaced along the length of the bank, and care was taken



Fig. 1. Dredge net used for sampling macroinvertebrates.

to stagger each sampling position so as to avoid covering a path taken by a tow from the opposite bank. The samples were preserved in 70 per cent alcohol.

Although the north and south samples ran parallel to each other in the middle of the dam, most of the animals would have come from the last part of the tow where the samples were effectively separated, because insects are generally more common in the shallower sections than in the deeper sections of dams (Barlow, pers. obs.). The experimental design meant that some of the later samples intersected the paths of earlier samples, but it was considered that this would not have seriously influenced the number of macroinvertebrates collected.

In the laboratory the samples were sorted to the lowest taxonomic level possible and counted. The effect of submerged grass (samples 9 to 13) and wind (samples 13 to 17) on the distribution of the community was examined using N (the total number of animals), S (the total number of taxa) and E (Heip's evenness). The distribution of the community was also examined using SAHN (sequential agglomerative hierarchical non-overlapping clustering programme) of the TAXON package (CSIRONET system). The data were then analysed to determine the number of samples required to estimate the true mean number of animals per sample with varying confidence intervals and degrees of precision. Statistical tests were conducted at the 5% level of significance.

TABLE 1. Numbers and types of macroinvertebrates in twenty samples collected with a dredge net in a farm dam in south-western New South Wales.

Dam bank orientation	West					North					East					South					Total number of specimens	Mean	Variance
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20			
Sample number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20			
Dytiscidae																							
<i>Allodessus bistrigatus</i> (Clark)	5	2	2	—	13	—	1	—	—	2	1	10	104	8	2	6	6	7	1	1	171	8.55	518.58
<i>Liodessus shuckardi</i> (Elk)	1	2	—	7	1	—	—	—	—	2	1	3	3	—	—	2	1	—	—	—	23	1.15	2.98
<i>Megaporus flonitii</i> (Clark)	—	—	2	1	1	—	5	4	2	1	—	2	—	3	1	3	4	—	4	—	33	1.65	2.77
<i>Antiporus giberti</i> (Clark)	17	20	7	16	34	18	7	9	7	4	—	7	2	13	18	1	2	1	15	21	219	10.95	78.37
<i>Antiporus fenoralis</i> (Boh)	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1		
<i>Eretes australis</i> (Erichson)	—	9	14	10	—	—	5	7	14	1	1	8	3	8	3	1	10	10	5	2	111	5.55	21.52
<i>Homoeodytes scutellaris</i> (Germ)	—	—	1	1	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	5		
<i>Sternopriscus multimaculatus</i> (Elk)	4	1	—	—	5	1	2	—	—	1	1	1	46	2	—	2	2	1	—	3	72	3.60	101.52
<i>Necterosoma wallastoni</i> (Clark)	—	14	8	4	3	1	8	8	13	—	4	4	9	5	4	—	1	6	3	7	102	5.10	16.41
<i>Rhantus suturalis</i> (Mael)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1		
<i>Hyphidrus elegans</i> (Montrouzier)	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	4		
Hydrophilidae																							
<i>Helochares</i> sp.	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	2		
<i>Spercheus</i> sp.	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1		
<i>Berosus</i> sp. a	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2		
<i>Berosus</i> sp. b	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1		
<i>Berosus</i> sp. c	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1		
(Specimens lost)	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2		
Hydraenidae																							
<i>Ochthebius</i> sp.	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2		
<i>Hydraena</i> sp.	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1		
Helminthidae																							
<i>Coxelmis V-fasciata</i> Lea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	2		
Corixidae																							
<i>Sigara</i> sp.	48	42	42	8	62	89	46	16	13	140	46	51	113	31	66	113	17	29	35	128	1135	56.75	1563.25
<i>Agraptocorixa parabiopunctata</i> (Hale)	37	7	15	12	38	26	21	12	5	45	21	6	6	20	21	11	3	1	5	25	337	16.85	157.82
<i>Agraptocorixa eurynome</i> (Kirkaldy)	2	3	4	4	12	4	6	5	4	37	2	14	21	7	2	18	5	8	3	8	169	8.45	73.84
<i>Micronecta annae</i> group	2	43	12	4	11	6	33	—	2	33	4	25	7	16	1	7	1	5	1	10	223	11.15	157.29
Nymphs	—	8	10	2	6	4	6	6	2	19	9	9	13	3	3	17	2	3	4	9	135	6.75	25.99
Notonectidae	53	10	7	16	29	30	15	15	29	74	50	17	40	37	93	32	12	17	58	112	746	37.30	824.64
Nepidae																							
<i>Ranatra dispar</i> Montandon	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	1	1	4		
Diptera larva	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1		
Trichoptera larva	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1		
Parastacidae																							
<i>Cherax destructor</i> Clark	4	2	—	2	4	3	2	1	2	5	4	11	2	5	9	12	—	—	1	4	73	3.65	11.82
Total number of individuals	173	164	124	81	225	188	159	86	95	364	145	170	373	169	225	225	68	88	136	332	3580	179.0	8146.42

RESULTS

The types and numbers of animals collected in each sample are listed in Table 1. The total number collected per sample did not diminish as sampling progressed, which justified our assumption in the experimental design that later samples would not have been influenced by their paths intersecting the paths of earlier samples. The variance was greater than the mean for all groups, indicating that a contagious (or clumped) distribution was shown by each group (Elliot, 1977). Clumped invertebrate populations are often described by the negative binomial model (Elliot, 1977). Consequently, chi-squared tests for goodness-of-fit of this model were conducted for the numerically dominant groups (*Antiporus gilberti*, *Sigara* sp., *Agraptocorixa parabiopunctata*, *Micronecta annae* group and Notonectidae) and for the total number of individuals in each sample. In all cases the χ^2 values were not significant (Table 2); thus the distributions did conform to the negative binomial model.

TABLE 2. The mean ($\hat{\mu}$) and dispersion parameter (\hat{k}) of the negative binomial distribution and χ^2 values for goodness-of-fit tests for the numerically dominant groups and for the total number of individuals in each sample, estimated by maximum likelihood methods using MLP © 1978 Lawes Experimental Trust, CSIRONET system. (The data had to be grouped because zero-frequency cells were not permitted in the programme; this resulted in different numbers of groups for each species and thus different degrees of freedom).

	$\hat{\mu}$	\hat{k}	χ^2	d.f.
<i>Antiporus gilberti</i>	11.31	1.22	6.26	6
<i>Sigara</i> sp.	56.77	1.89	4.35	3
<i>Agraptocorixa parabiopunctata</i>	17.80	1.68	5.22	4
<i>Micronecta annae</i> group	11.17	0.85	3.58	4
Notonectidae	33.92	2.16	1.38	5
Total number	173.47	4.10	8.46	9

The means, standard deviations and Mann-Whitney U-test statistics (Elliot, 1977) of N, S and E for the comparisons of grass-affected samples and wind-affected samples with control samples are given in Table 3. The U-statistics were not significant in any of the comparisons, which indicated that the distribution of the community was not influenced by submerged terrestrial grass or wind. This was confirmed by analysis of the data in Table 1 using SAHN, which did not reveal any obvious patterns of community distribution.

The minimum number of samples required to define the mean number of animals per sample was calculated using the formula of Elliot (1977);

$$N = \frac{t^2}{a^2} \left[\frac{1}{\bar{\chi}} + \frac{1}{\hat{k}} \right]$$

where N is the number of samples required, t is Student's t value for n-1 degrees

of freedom for a given confidence interval, a is the accuracy desired in describing the mean, \bar{x} is the mean of n samples, and \hat{k} is the dispersion parameter of the negative binomial estimated from:

$$\hat{k} = \frac{\bar{x}^2 - s^2/n}{s^2 - \bar{x}}$$

where s^2 is the variance of n samples. The values of N obtained using the information from Table 1 ($\bar{x} = 179.00$, $n = 20$, $\hat{k} = 3.97$) with various levels of accuracy and confidence intervals are given in Table 4.

TABLE 3. Means (\pm standard deviations) and Mann-Whitney U-test statistics of N (total number of animals), S (total number of taxa) and E (Heip's evenness), for the comparison of grass and control samples and wind and control samples. (Tabulated value of U at the 5% level of significance is 14 for $n_1 = 5$ and $n_2 = 15$; that is, a U -value less than 14 would be significant (Elliot, 1977)).

Parameter	Mean (\pm s.d.)	U_1	Mean (\pm s.d.)	U_2
	Grass		Control	
N	229.4 (± 129.9)	49	162.2 (± 70.91)	26
S	14.0 (± 1.87)	44	13.2 (± 1.37)	32
E	0.477 (± 0.121)	32	0.521 (± 0.137)	43
	Wind		Control	
N	210.0 (± 111.6)	28	168.7 (± 83.92)	48
S	14.4 (± 1.14)	58	13.1 (± 1.49)	17
E	0.471 (± 0.151)	32	0.522 (± 0.128)	44

TABLE 4. The number of samples required to estimate the true mean number of macro-invertebrates per sample in a farm dam with various levels of accuracy and confidence intervals

Confidence interval	Number of samples		
	$\pm 20\%$	Accuracy $\pm 30\%$	$\pm 40\%$
80%	12	6	3
90%	20	9	5
95%	29	13	8

DISCUSSION

A quantitative investigation of macroinvertebrate populations raises the problem of finding a suitable sampling technique. If the study concentrates on a single species, the sampling device most effective at catching that organism can be chosen. However, if the complete faunal assemblage is under investigation the sampling method chosen is a compromise, because the ability of different species to escape the sampling device varies. Consequently, interpretation of Table

MACROINVERTEBRATE SAMPLING-FARM DAM

1 is qualified by the ability of the different species to escape the dredge net. It follows that the data can not be used to determine absolute numbers of animals living on or above the substrate.

A contagious distribution is frequently seen in animal populations, because many environmental factors are unevenly distributed, and because some species have a tendency to aggregate and produce a contagious distribution without the influence of environmental factors (Elliot, 1977). In this study, neither wind nor the presence of submerged terrestrial grass appeared to influence the distribution of the macroinvertebrate community, which implies that these factors can be ignored when sampling similar dams with a dredge net. However, Crisp (1962) and Savage (1979) have suggested that the distribution of corixids in the littoral zone may be affected by wave action.

Elliot (1977) suggested that 95 per cent confidence limits and 40 per cent accuracy were acceptable in estimating the mean of benthic populations. In the present dam 8 samples would have given this result (Table 4). The number of samples required varies with the density of animals. As the study dam contained about an average number of insects for similar dams in the same region (Barlow, pers. obs.), it is suggested that when using a dredge net between 5 and 10 samples should be taken to obtain a statistically valid estimation of the mean number of animals per sample in these dams.

Qualitative sampling with plankton nets and an Ekman dredge did not reveal other macroinvertebrates than those retained by the dredge net. The dredge net can also be used in dams containing macrophytes by removing the kick chain and attaching a rake to direct weed under the net (Topp, 1967). Consequently, we conclude that the dredge net is probably the most suitable device for sampling macroinvertebrates living on or above the substrate in farm dams.

ACKNOWLEDGEMENTS

We would like to thank Ken Bock for assistance in collecting and analysing the samples, and the following people for identifying specimens: C. H. S. Watts (Dytiscidae, Hydrophilidae, Hydraenidae), J. Anderson (Hydrophilidae), E. B. Britton (Helminthidae), G. A. Holloway (Corixidae), T. A. Weir (Nepidae). Alan Jones gave helpful comments on the manuscript, and Pauline Wilson prepared the typescript.

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Effects of Environment upon Tortoise Pigmentation

R. W. DUNN

Royal Melbourne Zoological Gardens, Vic. 3052

ABSTRACT

An experiment lasting for six months, on two initially homogeneous sibling groups of young Krefft's tortoises, *Emydura krefftii*, showed that pigmentation in these tortoises was influenced by the colour of the substrate upon which they lived.

INTRODUCTION

Numbers of native and exotic tortoises are regularly bred at the Royal Melbourne Zoological Gardens. Hatchlings of aquatic species are usually housed in open-topped plastic containers for approximately the first year of life.

It has been observed that tortoises kept in containers of a light colour become consistently paler than typically coloured individuals of their species. Such pallor has been noted in Zoo-bred *Emydura krefftii*, *E. macquarii*, *Chelodina longicollis*, *C. expansa* and the terrestrial American box tortoise, *Terrapene carolina*. When some of these animals were transferred to darker coloured surroundings they soon resumed a normal hue.

Published descriptions of tortoise colouration by various authors suggest that although individual variation occurs, the colour of a particular tortoise does not change, and I have yet to read an account of colour change in tortoises. This suggestion has usually resulted in expressions of surprise or scepticism. To resolve the matter, I carried out a simple experiment on *E. krefftii* over a six-month period. Typical carapace colouration of *E. krefftii* is described as "dark brown" (Worrell, 1964), and "brown to dark brown above" (Cogger, 1975).

MATERIALS AND METHODS

Two-glass fish tanks, each measuring 30 x 20 x 20 cm were used for the experiment. To provide contrasting floor colours, a sheet of white paper was placed beneath the transparent base of one tank, and a piece of rigid black plastic was cut and fitted inside the other.

The tanks were partly filled with tap water which was maintained for the duration of the experiment at 25-27°C.

On 19/11/79 four individuals of *E. krefftii*, similar in colour and size, were selected from a clutch of eighteen hatched five weeks earlier, and these were housed two to a tank. At this stage the young tortoises were of a medium grey-brown colour and very conspicuous against the black and white floors of their respective tanks.

Within the tanks, conditions, with the exception of the floor colours, were kept as alike as possible. Water depths and temperatures were identical, as was the food given to the tortoises (finely chopped raw meat and fish, live daphnia, mosquito larvae and house-fly pupae). A small block of plaster-of-Paris was immersed in each tank to ensure dissolved calcium levels adequate for healthy shell growth. A flowlux aquarium light, suspended 30 cm above the tortoises, was switched on at 8.15 a.m. for approximately $7\frac{1}{2}$ hours daily.

RESULTS

Within seven days of commencing the experiment a colour difference between the two groups was apparent. The tortoises in the black-based tank (Group A) were uniform grey-brown, while those of Group B were paler, with a few dark spots on the dorsal surface and a line of darker pigment around the periphery of each carapace scute, forming a reticulate pattern.

One month later the difference was distinct. Group A animals had become considerably darker and those of Group B were more pallid. In both groups the skin of the head, neck and limbs, as well as shell scutes, was affected. Six months from commencement of the experiment, the contrast between the two groups was quite dramatic. Group A animals had become a dark slate grey colour while those of Group B had faded to a light fawn.

At this stage the two groups were photographed, (Fig. 1), and the four tortoises returned to the company of their siblings in a large, neutral coloured tank. Within one month the pallid tortoises had reverted to the grey-brown colour of their companions, while the dark individuals required approximately twice this period of time before they too became virtually indistinguishable from their siblings.

DISCUSSION

The hard exoskeleton of adult Australian tortoises provides effective protection against most predators, but juveniles of all species appear to be vulnerable to attack from predatory birds, reptiles (Goode, 1967) and eels and other fish (Cann, 1978), and their survival depends largely upon their ability to avoid detection.

In Australia, tortoises are found in a wide range of aquatic habitats including rivers, water-holes, swamps and billabongs. The substrates of various water-bodies may differ greatly, ranging from black mud to white sand. The ability to

EFFECTS OF ENVIRONMENT UPON TORTOISE PIGMENTATION

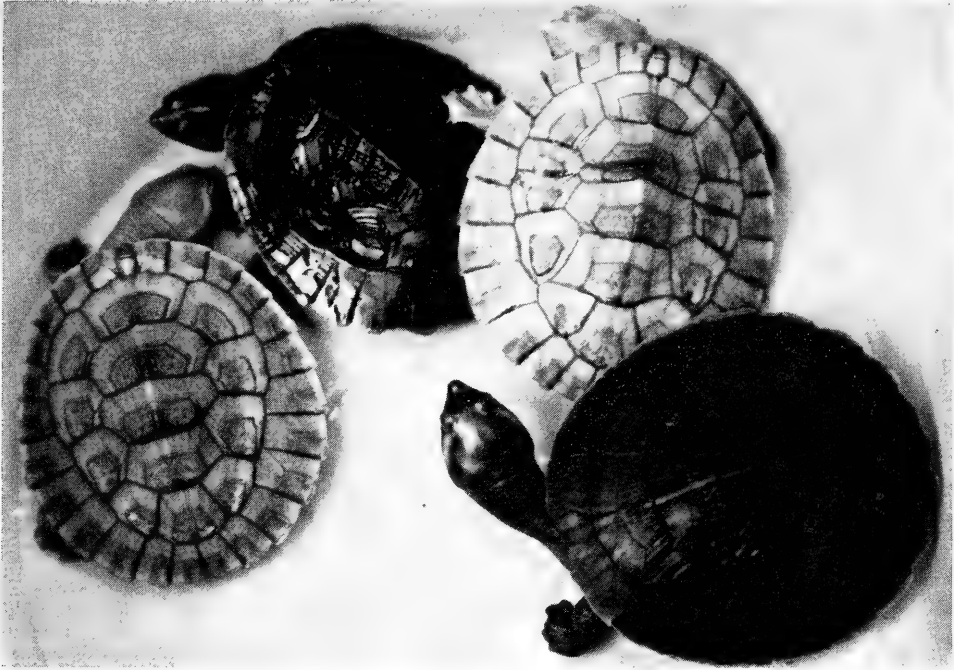


Fig. 1. Young *Emydura krefftii* reared for six months in a white-floored container (Nos. 1 and 3 from left) and a black-floored container (Nos. 2 and 4).

assume cryptic colouration consistent with a particular substrate has obvious advantages for tortoises, increasing an individual's chances of avoiding predation and allowing effective exploitation of a wider range of habitats by the species.

In view of its survival value it is therefore not surprising to find that the pigmentation of juvenile tortoises, at least of some species, is capable of modification.

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The Status, Distribution and Abundance of *Dasyurus maculatus* (Tiger Quoll) in Australia, with particular reference to Victoria

IAN MANSERGH

Arthur Rylah Institute for Environmental Research, P.O. Box 137, Heidelberg, Victoria 3084.

ABSTRACT

Dasyurus maculatus (Tiger Quoll) is considered to be an uncommon to rare animal on the Australian mainland. However, it is apparently more common in Tasmania and some areas of northern New South Wales. It is very rare or extinct in South Australia. The species inhabits a variety of forest types along the Great Dividing Range and is most commonly found in areas where the mean annual rainfall exceeds 600 mm. The range of the species on the mainland has been reduced. For example, since European settlement of Victoria the range of this species has been reduced by about 50% and is now disjunct. *D. maculatus* is now a rare animal in Victoria and the most important areas for its conservation are East Gippsland, the Otway Range and around the "Stones" in the southwest of the state. Factors presumed to have been involved in its decline include habitat destruction and the widespread use of trapping and poisoning. More research into the ecology of the species is required.

INTRODUCTION

Dasyurus maculatus (Tiger Quoll or sometimes known as Tiger Cat) is the largest marsupial carnivore extant on the mainland of Australia and its previous range included Tasmania, South Australia, Victoria, New South Wales and Queensland (Fig. 1). Information concerning this species is scant. For areas where documentary evidence (both scientific and general literature) exists regarding its occurrence it appears that *D. maculatus* was not a common animal during the first century of European settlement in Victoria and other states. This is in contrast to *D. viverrinus* (Eastern Quoll or sometimes known as Eastern Native Cat) which was relatively common in many areas (Fleay, 1932; Wakefield, 1954). All accounts which suggest that *D. maculatus* was common in Victoria are considered by the author to be questionable because the records are invariably associated with emotive circumstances, for example the killing of poultry, or remain ambiguous because *D. maculatus* and *D. viverrinus* are both discussed as "native cats" (e.g. Morrison, 1948a and b).

The rarity and declining status of *D. maculatus* in Victoria was noted by Fleay (1932). It has been suggested that the species suffered from a disease, similar to that believed to have caused the dramatic decline of *D. viverrinus* early this century. However no direct documentation is available on this (Jones, 1923; Lewis, 1934; Caughley, 1980). Habitat destruction, persecution and the widespread trapping and poisoning in and around forested areas may have been more important factors in the decline of *D. maculatus* in Victoria than the presumed disease.

Begg (1981) noted the dearth of knowledge concerning *Dasyurus* spp. However, his research on *D. hallucatus* (Northern Quoll), and Godsell's (1982) study on *D. viverrinus* have added greatly to our knowledge of the genus. No recent substantial studies of *D. maculatus* have been undertaken in Victoria. Discussion of the distribution and abundance of the species frequently relies on comments such as those given by Fleay (1948). In an attempt to rectify this situation I have reviewed in detail the currently available data on the status, distribution and abundance of *D. maculatus* in Victoria and have compiled the most recent parallel data for other states (e.g. Caughley, 1980).

METHODS

Data were compiled from the literature, records held by the Fisheries and Wildlife Division of Victoria (FWD), all major museums in Australia, the British Museum (National History), the Victorian Department of Crown Lands and Survey (DCL&S), the Victoria Archaeological Survey and the Royal Zoological Gardens, Melbourne. Details provided by local residents of Gippsland, the Otway Range area and southwestern Victoria were also used. Past and present dog trappers (employed by Department of Crown Lands and Survey for trapping wild dogs) were interviewed. Localities, dates of capture and other information were compiled from all reliable records.

Records of the Fisheries and Wildlife Division concerning *D. maculatus* were derived from one of three sources: files containing memoranda, correspondence and newspaper articles. Annotated data sheets of specimens or sightings and trapping records of the Wildlife Survey Unit were also used. The latter records, collected since 1973, were derived from several extensive fauna surveys conducted on public land south of the Great Dividing Range (Emison *et al.*, 1975, 1978; Norris *et al.*, 1979, 1983, pers. comm.; Menkhorst and Gilmore, 1979; Menkhorst and Beardsell, 1982). Over 75,000 trapnights were completed during these surveys, the majority of which were undertaken using wire cage traps (30 cm x 20 cm x 16 cm) baited with a mixture of peanut butter, rolled oats and honey. Such traps and bait are known to capture at least juvenile *D. maculatus* (Emison *et al.*, 1978), and therefore would be able to capture juveniles from about October through to the end of March. One record was derived from a Wildlife Survey Unit *D. maculatus* trapping program (280 trapnights) in which wire cage traps (25 cm x 25 cm x 70 cm) were

DISTRIBUTION AND ABUNDANCE OF DASYURUS IN AUSTRALIA

baited with a variety of baits including fish, *Macropus giganteus* (Eastern Grey Kangaroo), sheep livers, roadkilled *Platycercus elegans* (Crimson Rosella) and dead rabbit which had its fur singed. A single animal was caught on a piece of singed rabbit.

The distribution of *D. maculatus* sightings and captures was plotted on a grid map of Victoria (5 minutes latitude by 5 minutes longitude). In evaluating distribution, records were temporarily grouped as pre-1960, 1960-69, and 1970-79. The recent records took precedence where records from different periods were coincident. Records were also sorted by date, into decade of occurrence. Records of the species in Tasmania, South Australia, New South Wales and Queensland were compiled from the most recent literature (e.g. Kitchener *et al.*, 1981) and consultation with

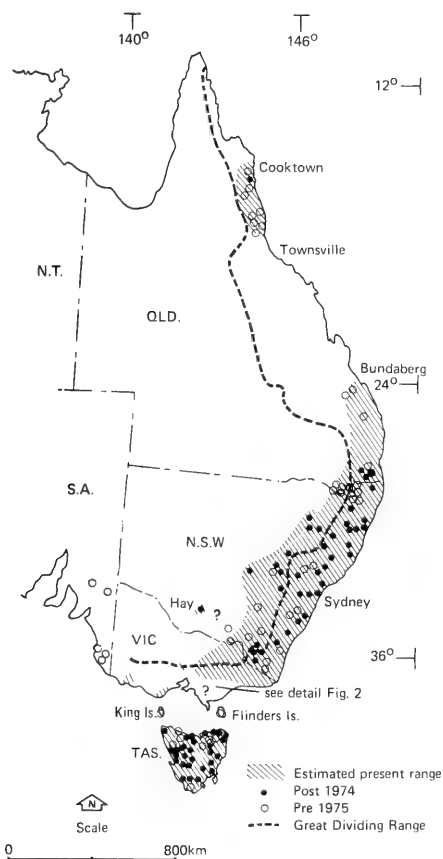


Fig. 1. The Australian distribution of *D. maculatus* showing recent (post-1974) and past (pre-1975) records.

the respective museums. Other records collected by the author have also been included. To conform to other studies (Caughley, 1980) these data were temporarily grouped pre-1975 and post-1974 (Fig. 1).

RESULTS AND DISCUSSION

Results are summarised in Table 1 and Figures 1, 2 and 3. They show past and present distribution of *D. maculatus* in Australia and Victoria, areas in Victoria where *D. maculatus* is now most frequently recorded and the temporal distribution of twentieth century records collected in Victoria. A bibliography of the 185 references examined is lodged in Fisheries and Wildlife Division, File 93-1-42. A resumé of the status, distribution and abundance is provided for all states where the species is known to have occurred.

The Tiger Quoll is limited to eastern Australia and the previous range approximated the areas that receive a mean annual rainfall in excess of 600 mm, (see Fig. 2 for Victoria) the notable exception is the northern Queensland population where

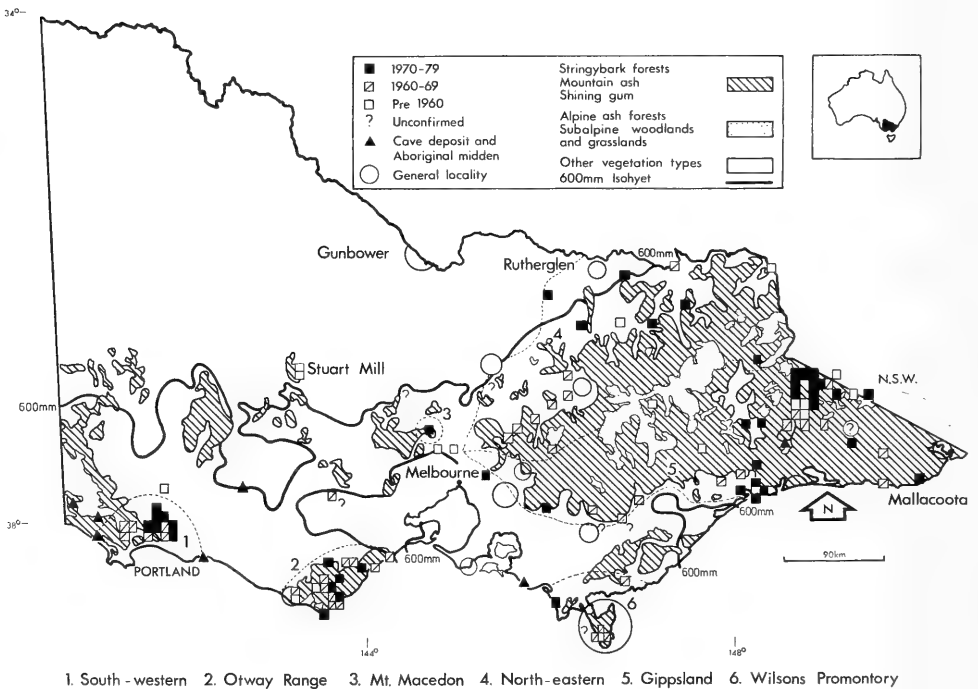


Fig. 2. The Victorian distribution of *D. maculatus* showing 600 mm isohyet.

DISTRIBUTION AND ABUNDANCE OF DASYURUS IN AUSTRALIA

the species appears to have been limited to areas that received a mean annual rainfall in excess of 1000 mm. Within this range the species inhabits Closed forest, Tall open-forest, Open-forest and is occasionally recorded in Woodland (Specht *et al.*, 1974).

TASMANIA

The distribution of *D. maculatus* is patchy in Tasmania with most records occurring in the Closed forest and Tall open-forests (Specht *et al.*, 1974) of the western highlands and the northeastern and northwestern regions (Green, 1973). Sub-fossil remains of *D. maculatus* have been recorded on King, Flinders and Cape Barren Islands in Bass Strait. Spencer and Kershaw (1910) erected *D. bowlingi* as a Tiger Quoll endemic to King Island and possibly Deal Island, however, Marshall and Hope (1973) concluded that this species was conspecific with *D. maculatus*. The species is now extinct on King Island (most recent sighting 1923) and 'very rare' on the other islands (Hope, 1972). As elsewhere, *D. maculatus* is not as common as *D. viverrinus*, however, there is anecdotal evidence to suggest that both species are recovering from a population decline earlier this century (Andrews, 1981; Godsell, 1982; Green, 1973; Munday, 1966). *D. maculatus* is regarded as common to uncommon in Tasmania (Green, Queen Victoria Museum and Art Gallery and Andrews, Tasmanian Museum and Art Gallery, pers. comm.) and the most recent record is from "The Churn", Franklin River, January, 1983 (pers. obs.).

SOUTH AUSTRALIA

The species was never common in South Australia and was restricted to the forests of the coast and the southeastern region of the state. Jones (1923) noted

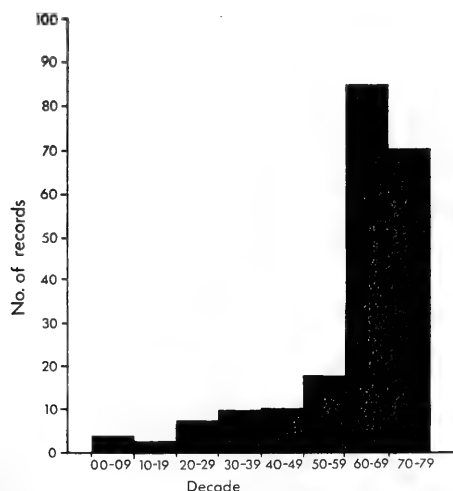


Fig. 3. Records of *D. maculatus* in Victoria by decades since 1900 (221 records).

that there was then still a possibility that the species persisted in the state, however, the most recent specimen is from Barmera, dated August 1958 (S.A. Mus. No. M6187). The species is very rare or extinct in the state. Large areas of the previous range have been converted to pine plantations. The nearest, confirmed present range is in Victoria approximately 100 km from the South Australian border (Fig. 2).

TABLE 1. The number of five-minute blocks in various regions of Victoria that have recent records (post 1959) of *D. maculatus* (unconfirmed Wilsons Promontory records appear in brackets).

Region	Number of post-1959 records in five-minute blocks			
	1	2-3	4-5	6-8
Southwestern	8	3	1	1
Otway Range	10	3	2	1
Mt. Macedon	1	0	0	0
Northeastern	16	2	0	0
Gippsland	28	7	1	4
Wilsons Promontory	1(4)	1	—	—

NEW SOUTH WALES

Records of *D. maculatus* are concentrated on both sides of the Great Dividing Range and one specimen has been recorded as far west as Hay (Fig. 1, Caughley, 1980; Marlow, 1958; Troughton, 1954). Caughley (1980) provides a map of the recent records of the species and regards the species as uncommon in New South Wales although the status varies from region to region and it is more common in the north of the state (Settle, 1978; Calaby, 1966; Scott, 1975). Settle (1978) noted that the destruction of forested areas has greatly reduced the available habitat for this species in the state. The magnitude of the range reduction appears less than in Victoria, however, the population around Hay is probably isolated (Caughley, 1980; Marlow, 1958).

QUEENSLAND

The distribution of the species in Queensland is disjunct (Fig. 1) with some authors (e.g. Settle, 1978) according the isolated population between Cooktown and Townsville sub-specific status, *D.m. gracilis* (see Ramsay, 1888). The species is regarded as uncommon in the state, however, any reduction in range since European settlement has not been established (Van Dyck, Queensland Museum, pers. comm.). The most recent museum specimen was collected at Mt. Spurgeon in 1974 although there have been more recent reports from Lamington Plateau; Gatton, Mt. Lindesay Highway and Thornton Peak (Van Dyck, Queensland Museum, pers. comm.).

VICTORIA

Past distribution. The range of *D. maculatus* in Victoria at the time of European settlement included areas where the mean annual rainfall exceeded 600 mm (Fig. 2). This area, centred on the Great Dividing Range, corresponds to the original distribution of forest types dominated by medium to tall eucalypts, i.e. >10 m (Everett, 1869; Carnahan, 1976). The record from Gunbower in the 1880's (Morrison, 1945) appears anomalous but it is likely that the riparian vegetation along the Murray River provided a corridor of suitable habitat (Kile *et al.*, 1980). Such a conclusion appears to be supported by a record in the Rutherglen area in 1895 (McEvey, 1965) and South Australian records along the Murray River. Thus the perceived range of *D. maculatus* at the time of European settlement, including the corridor to Gunbower, included 60% of Victoria.

Present distribution. Since European settlement, the range of *D. maculatus* in Victoria has contracted and is now disjunct (Fig. 2). Populations in southwestern Victoria, the Otway Range and, probably, Mt. Macedon and Wilsons Promontory are now isolated though the continued presence of *D. maculatus* in the two latter regions is uncertain. The species was observed on Wilsons Promontory in 1902 (Kershaw, 1940) and Fleay (1948) released two pairs in the area in late 1939. Norris *et al.* (1979) commented that subsequent records required confirmation (e.g. McQueen, 1960); these authors were unaware of the recent sightings from Cape Liptrap (Land Conservation Council of Victoria, 1980) and Port Franklin (C. Rossiter (Hedley) pers. comm.). It seems possible that the species may persist in this region. Similarly, its status in the Mt. Macedon area is uncertain because there is only one recent record from this locality. This locality is isolated from the contiguous forest of the Great Dividing Range (Fig. 2).

Since European settlement, the area covered by forest and dense woodland in Victoria has been reduced from about 74% to about 33% (Kile *et al.*, 1980). *D. maculatus* has been recorded in 2.8% (97) of the 3364 5-minute blocks in Victoria. However, in recent times (post-1959) they have been recorded in only 42 of these blocks. These data support the view that the range of *D. maculatus* has been halved in the last 140 years and its range now includes only about 30% of the state (Fig. 2). Within this range there are three areas in which records are concentrated, namely southwestern Victoria, especially the area around the "Stones" (Emison *et al.*, 1978), the Otway Range, especially the area bounded by Lavers Hill, Cape Otway and Deans Marsh (see Emison *et al.*, 1975) and the upper Snowy River valley above Tulloch Arch Gorge (Norris and Mansergh, 1981).

Habitat. Specht *et al.* (1974) identified 24 broad vegetation alliances in Victoria and *D. maculatus* has been recorded in at least four of these, i.e. Tall open-forest, Open-forest, Low open-forest and Woodland. It has also been recorded from areas local residents describe as "rainforest" (= Closed forest). *D. maculatus* is sometimes trapped on farmland, however, such localities are almost invariably near areas of forest. *D. maculatus* has been recorded moving more than 2 km overnight (H.

Bass (Tubbut) pers. comm.) and animals, usually males, taken outside forested areas are presumed to have wandered from their preferred habitat during the breeding season (Mansergh, 1983).

Abundance. It is difficult to establish the past and present abundance of *D. maculatus* for many reasons. One of the main reasons is that the 240 records are not the result of systematic field surveys. Few, if any, of the wide variety of factors influencing the number of records during this century (Fig. 3) have remained constant. In this period land use changes have certainly been extensive. Interest in, and efforts to record the abundance of, wildlife generally have increased suggesting that early estimates of abundance would have been based on poorer records. Furthermore, in discussing the status of dasyurids, Archer (1979) noted the difficulty of determining whether rarity is normal, either as a steady state or at a specific point within a periodic fluctuation or, alternatively, indicative of an abnormal decline (see Hollings, 1973). Despite these limitations, changes in relative abundance may be estimated by consideration of pre-European distribution, factors that may have affected the population since European settlement and estimation of the abundance at present.

Fossil record. Data derived from seventeen Pleistocene and Holocene cave deposits in Victoria were provided by Wakefield (1964, 1967a and b). In these deposits *D. viverrinus* was recorded more frequently than *D. maculatus* (95% and 65% respectively), and in only two deposits were the remains of *D. maculatus* more numerous than *D. viverrinus*, both of these caves being in close proximity to areas where *D. maculatus* is still present, i.e. southwestern Victoria and the Otway Range. Interpretation of these data is difficult as at least some of the deposits were at owl roosts (e.g. Wakefield 1967a) and as a fully grown *D. viverrinus* is about half the weight of *D. maculatus* it would therefore have been preferred prey.

EUROPEAN SETTLEMENT TO 1960

One of the earliest accounts of *D. maculatus* in Victoria is provided by Wheelwright (1861) who believed the species to be rare and only sparingly dispersed through thick bush. Other accounts of the 19th century are in accord with this estimation (Batey, 1907; Wakefield, 1954). In the 1880s John Hallifax (1934) trapped "about 100 native cats for every tiger cat". Certainly, for a time in the late 19th century, 2000-5000 *D. viverrinus* skins were exported annually to England from Australia, but since the skin of *D. maculatus* had no commercial value comparative statistics are not available (Poland, 1892).

PRESENT (POST-1960)

Data presented in Figure 3 show a marked increase in the frequency of records since 1960. However, this is almost certainly an artifact of increased trapping and collection rather than an indication of increased numerical abundance as suggested by Hyett and Shaw (1980). For example, active documentation of records of *D. maculatus* by Fisheries and Wildlife Division only began in 1959. Only ten 5-minute

blocks in Victoria (0.3%) have more than four recent records (Table 1) suggesting that *D. maculatus* is not an abundant animal. Furthermore, only four animals have been trapped and one sighted during the surveys conducted by Wildlife Survey Unit since 1973 (see Methods).

In a mammal survey, conducted over 2400 km² in the Upper Richmond and Clarence Rivers region (NSW), Calaby (1966) sighted one animal and, with the co-operation of local residents, recorded 13 animals over a three-year period. The highest frequencies recorded from each of the three Victorian areas described above (Distribution section) over any three-year period are: 10 in the Otway Range (1969-71), six in the Upper Snowy River area (1970-72) and six in the south-western area (1966-69).

FACTORS INFLUENCING ABUNDANCE

In 1935, *Dasyurus* spp. were afforded legal protection (Victorian Government Gazette, 1935) because of a dramatic decline in numbers earlier this century (Lewis, 1934). Nevertheless, documents of the period that relate the decline of *D. maculatus* to an earlier epidemic disease invariably use the generic term native cat.

Previous authors (e.g. Caughley, 1980) have suggested that the introduced disease toxoplasmosis may have caused a decline in *D. maculatus* around the turn of the century. However, there is little direct evidence to support this suggestion (Munday, 1966; Collins, 1973; Green, 1973; Attwood *et al.*, 1975; Caughley, 1980). Furthermore, as *D. maculatus* has always been rarely observed in Victoria it appears unlikely that a population decline of the magnitude that affected *D. viverrinus* would have been noticed.

There may be other explanations for the decline of *D. maculatus* rather than the introduction of an exotic disease. For example, Batey (1907) observed the demise of *D. viverrinus* and noted that (p.72):

"In 1846 this animal was very numerous, but later at various periods they seemed to be infested with a burrowing maggot which brought them almost to the verge of extinction, and it was sometime before they again regained their numerical strength, but I do not think the attacks of this parasite would alone have sufficed to complete their extinction . . . later on, when the rabbits became plentiful, and had to be trapped many native cats were caught in the traps".

Specimens of *D. maculatus* sent to the Fisheries and Wildlife Division since 1959 (the commencement of *D. maculatus* data sheets) have been frequently infested with the parasitic larvae of the native flea *Uropsylla tasmanica* (Warneke, pers. comm.) and such an affliction is similar to that described by Batey (above) and Fleay (1932). It is not known whether the prevalence of this flea depends on the population density of the host and, consequently, whether such infestations are part of a normal population cycle or are a result of abnormal event(s) acting on a

weakened host population. Consequently the effects of *U. tasmanica* on the past and present population(s) of *D. maculatus* remain unknown.

Both feral cats (*Felis catus*) and foxes (*Vulpes vulpes*) may compete with the Tiger Quoll for food resources (see Brunner *et al.*, 1981), however, the absence of a quantitative analysis of the diet of the Tiger Quoll precludes a definitive answer to this question. It is noteworthy that in Tasmania, the state where both the Tiger Quoll and Eastern Quoll are most abundant, there is no feral fox population. In Tasmania the density of the feral cat population appears to be related to the abundance of rabbits (*Oryctolagus cuniculus*) a favoured food item (Green, 1973).

A combination of habitat destruction and the widespread trapping and poisoning in and around forested areas (e.g. Douglas, 1959; Calaby, 1966; Rolls, 1969; McIlroy, 1981; Settle, 1978) were probably responsible for the extinction of *D. maculatus* in many areas. Anecdotal evidence gives varying times for local disappearances and reappearances of *D. maculatus* (e.g. McEvey, 1965; Baade, 1925).

STATUS AND CONSERVATION

At the time of European settlement the range of *D. maculatus* included five states. It is now considered very rare or extinct in South Australia, rare in Victoria, uncommon in Queensland and common to uncommon in New South Wales and Tasmania. Some of the problems associated with the conservation of the species in Victoria are discussed below, however, it is considered by the author that similar problems occur in other parts of its range.

The range reduction in Victoria has probably been caused by a number of factors, the major one being habitat destruction. The precise habitat requirements of *D. maculatus* are not known, although it is dependent upon the remaining forested areas (Fig. 2). It is important that areas where *D. maculatus* is frequently recorded, i.e. around the "Stones", Otway Range and East Gippsland, receive adequate protection. Existing National Parks and Wildlife Reserves are probably inadequate (e.g. Norris and Mansergh, 1981). It is also notable that in February 1983 severe and extensive bushfires occurred in the Otway Range, Mt. Macedon and East Gippsland areas. The latter fire covered a forested area of over 2000 km².

In Victoria, the conservation status of the four vegetation alliances (see Habitat section) in which *D. maculatus* has been recorded, vary from "nil to reasonable" (Specht *et al.*, 1974). Forests and dense woodland now cover about 33% of Victoria (Kile *et al.*, 1980), however, only 2% of forests in Victoria are in National Parks whilst 41% are designated as State Forest, 47% are gazetted in other public land categories over which the Forests Commission of Victoria retains timber rights and 10% of forests are privately owned (Australia, Senate, 1981).

Furthermore, as no comprehensive system of corridors between reserves has been incorporated into the reserve system there is a possibility that the Victorian

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populations of *D. maculatus* will be further fragmented. It is therefore important that land uses outside the reserve system do not destroy extensive areas of *D. maculatus* habitat.

Major land use changes, involving clearfelling of the native forest, have been proposed for several regions where *D. maculatus* is most frequently recorded, i.e. East Gippsland (Scott, 1981) and Otway Range (Forests Commission of Victoria, 1981). The effects of these practices on *D. maculatus* have not been studied, although adverse effects on potential food sources and reduced availability of breeding hollows occur (Recher *et al.*, 1980). The species occurred in the Boola Boola State Forest last century and was recorded near the edge of this forest in 1966. However, in a study of the effects of clearfelling on wildlife in Boola Boola State Forest, Loyn *et al.* (1980) found no evidence that the species still occurred in the area. Elsewhere clearfelling and related land use practices in forested areas have caused concern for the survival of *D. maculatus*, for example in Tasmania (Patterson, 1977). Recher *et al.* (1980) obtained only one locality record in a five-year study of the Eden woodchipping region, where it was previously described as possibly endangered (Scott, 1975).

As the majority of the species' range currently occurs outside reserves it is important that land management be orientated towards ensuring the persistence of the species in these areas. However, management strategies can only be evaluated after a basic knowledge of the ecology of the species is obtained.

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Burrowing behaviour and associated hindlimb myology in some Australian hylid and leptodactylid frogs

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ABSTRACT

Two different modes of backwards burrowing have been observed amongst Australian leptodactylid frogs namely 'circular' and 'backwards sliding'. One of these modes is found also amongst hylid frogs. Analyses of the myology of the hindlimb of these species shows that the circular burrowing species *Notaden nichollsi*, *N. melanoscapus* and *Neobatrachus* sp. show increased mass in the muscles of the lower limb, and considerable modification of the *M. cruralis* when compared with the 'backwards sliding' burrowing species *Limnodynastes ornatus* and *L. dumerilli*. 'Backwards sliding' burrowing and associated muscular development was observed also in the hylid species *Litoria alboguttata*, *Cyclorana australis* and *C. longipes*.

INTRODUCTION

The burrowing habit is widespread amongst Australian frogs. It enables species with highly permeable skins to inhabit areas that become arid for long periods during the year. Two methods of burrowing are known — backwards and frontwards. Backwards burrowing frogs use the hind feet to scrape away the soil underneath them and then manoeuvre themselves into their hole, rear end first. Such frogs have enlarged metatarsal tubercles (sometimes keratinised) on the plantar surface of the foot. Frontwards burrowing frogs use the forelimbs to dig a hole, into which the head is pushed. The forelimbs then actively propel the animal into the ground (Emerson, 1976; Tyler *et al.*, 1980).

The backwards burrowing habit is the more common and is thought by some to have developed from frogs pressing themselves into the soil to avoid water loss, while waiting to catch prey (Hillenius, 1976). In this manner the body became buried first and the head remained exposed.

Amongst Australian frogs the backwards burrowing habit is exhibited by members of the families Hylidae (*Cyclorana* spp., *Litoria alboguttata*) and Leptodactylidae (*Notaden* spp., *Neobatrachus* spp., *Limnodynastes* spp., *Uperoleia* spp. and *Heleioporus* spp.).

The hylid backwards burrowers are restricted to the north and north-eastern parts of Australia whilst backwards burrowing leptodactylid species are found throughout the continent. Amongst the leptodactylid genera, frontwards burrowing has been observed only in the myobatrachine frogs, *Myobatrachus gouldii* and *Arenophryne rotunda* restricted to the west coast of Western Australia (Main *et al.*, 1959; Tyler *et al.*, 1980).

Little has been published on the behaviour and associated morphology of Australian burrowing frogs. Walpole (1964) discussed the behaviour and subterranean activity of *Neobatrachus pictus* but did not include any associated morphological data. Packer (1963) examined the burrowing behaviour of *Heleioporus eyrei* under various light and moisture regimes. Emerson (1976) has produced the most detailed study to date of the behaviour and morphology of both the North American backwards burrower *Glyphoglossus molossus* (Microhylidae) and the African frontwards burrower *Hemisus marmoratus* (Ranidae).

This paper examines the burrowing behaviour and associated morphology of a number of Australian backwards burrowing frogs of the families Hylidae and Leptodactylidae.

MATERIALS AND METHODS

BURROWING BEHAVIOUR

Species selected for burrowing observations were: *Cyclorana australis*, *C. longipes*, *Litoria alboguttata*, *Notaden nichollsi*, *N. melanoscaphus*, *Neobatrachus* sp., *Limnodynastes ornatus* and *L. dumerili*.

Each frog was placed on a fine sand substrate in a shallow glass aquarium. A 40 watt light source was placed directly over the aquarium to induce burrowing. Observations were made on direction of burrowing, and use of limbs. Film was taken of burrowing behaviour of *Notaden nichollsi*, *Limnodynastes ornatus*, *L. dumerili*, *Cyclorana australis* and *C. longipes* using a Canon 8 mm movie camera. *Hindlimb myology*: The muscles of the hindlimb of the following species were investigated (numbers in parentheses indicate the number of specimens examined): *Cyclorana australis* (10), *C. longipes* (2), *Litoria alboguttata* (2), *L. caerulea* (2), *L. nasuta* (1) (Hylidae); *Notaden nichollsi* (2), *N. melanoscaphus* (2), *Limnodynastes dumerili* (2), *L. ornatus* (2), *L. tasmaniensis* (1), *Neobatrachus* sp. (1) (Leptodactylidae). Subjects for study were determined by the availability of material maintained at the University of Adelaide.

External measurements taken prior to dissection, following the method of Tyler (1968), were: snout to vent length (S-V), tibia length (TL), head length (HL), head width (HW), eye to naris distance (E-N), internarial span (IN), eye diameter (E), tympanum diameter (T). Also taken were foot length (FL) from tip of longest toe to articulation of astragalus calcaneum with tibiofibula

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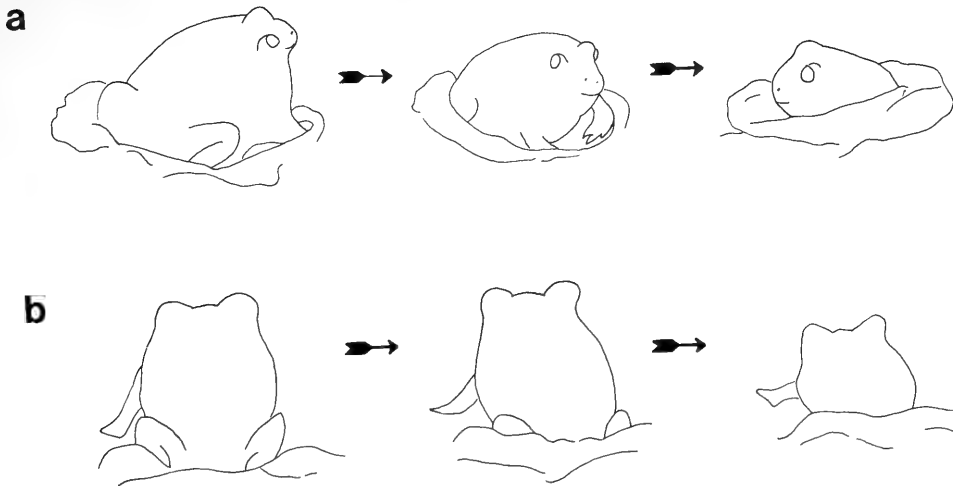


Fig. 1. Burrowing movements in (a) circular burrowing and (b) backwards sliding species.

and foot width (FW) at widest point. Measurements were read to 0.01 mm using dial callipers.

Muscle descriptions follow the terminology of Dunlap (1960). Measurements of length (L), thickness (T), and width (W) of individual muscles were taken using dial callipers. Length was measured from origin to insertion of each muscle, width at the widest point of each muscle, and thickness at the midpoint of each muscle. Measurements were expressed as a ratio of snout to vent length, thigh length, or tibia length.

Limits of intraspecific variation in the qualitative and quantitative description of muscles were established initially by an examination of ten specimens of *Cyclorana australis*. In this species muscle measurements were analysed for intra-specific variability using the method of Keough and Butler (in press). We excluded from consideration in all other species those measurements that in *C. australis* exhibited substantial variability. Hence the analysis is confined to those measurements that have a low intrinsic variability. Dissection was aided by topical application of the iodine/potassium iodide solution of Bock and Shear (1972).

All specimens examined had been killed in a relaxed state using chloral hydrate solution, fixed in a similar pose and preserved in 65% alcohol. It was felt that descriptions were comparable, and that there was no variability attributable to distortion following different fixation of specimens.

Illustrations were made using a Wild M5 stereo-dissecting microscope with attached camera lucida. Superficial and deep muscles were illustrated separately. For illustrations of deep musculature the following muscles were removed: *M. gluteus magnus*, *M. tensor fasciae latae*, *M. semimembranosus*, *M. ileo-fibularis*, *M. sartorius*, *M. adductor longus* and *M. adductor magnus* (ventral belly). Part of the vent has also been removed in all illustrations in order that the origins of some muscles could be seen more clearly.

RESULTS

BURROWING BEHAVIOUR

The general mechanism of burrowing for each species examined is backwards motion into the soil, using the feet in a scooping action. The sequence of movements is as follows:

- (1) From a resting position the body is raised up on the forelimbs.
- (2) One leg is retracted and closely folded while the other leg and forelimbs support the weight of the frog.
- (3) As the leg is folded the tibia is slightly elevated above the femur.
- (4) The foot is inverted.
- (5) The leg is extended slightly from the knee and ankle joints.
- (6) While this is happening the foot is everted bringing the metatarsal tubercle in a scooping motion to the surface of the substrate, gouging a hole and moving the substrate to one side of the frog.
- (7) Steps 2 to 6 are repeated from one to four times.
- (8) The other leg is then used as in steps 1 to 7, while the opposite leg supports the frog. Using this method a depression is created at the rear end of the frog into which it moves.
- (9) When each leg has been used alternately from two to five times, the forelimbs and hindlimbs are used to push the frog into the hole formed by digging. (Fig. 1b).

(i) *Backwards-sliding burrowers*

In these frogs the sequence of burrowing expressed in steps 1 to 9 was followed. The frog may pause or may continue with the burrowing and sequence 1 to 9 then is repeated.

As the frog gets deeper it may push its body sideways so that the soil built up on each side falls, so covering the frog. These frogs would shift their direction of burrowing slightly if their feet met resistance such as a stone, or compacted soil. The general direction of burrowing is at a slight angle to the surface. Once most of these frogs are covered by the substrate they cease to burrow.

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This type of burrowing (Fig. 1b) occurs in *Cyclorana australis*, *C. longipes*, *Litoria alboguttata*, *Limnodynastes ornatus* and *L. dumerili*.

(ii) *Circular burrowers*

These frogs also burrowed with leg movements described in steps 1 to 9. However, the forelimbs were used not only to push the frog backwards into the hole, but to pivot the animal as well, turning it around in the hole so that it faced in a different direction, with a new area of substrate under its feet. The frogs may turn clockwise or anticlockwise, and up to 180° in a turn. If turning clockwise, the left forelimb seems to provide the greatest force pushing against the substrate, and if turning anticlockwise, the right forelimb is used. Both forelimbs and hindlimbs are used in turning the animal.

The frog may continue turning in one direction or may turn back and go in the other direction. One specimen of *Neobatrachus* sp. usually completed a full circle before being completely buried.

The burrowing sequence is as follows:

Sequence 1 to 9 as above.

- (10) After the legs are used alternately, the forelimbs are used to push the frog back into the hole and to rotate it in a clockwise or anti-clockwise direction. The feet are also used to help rotate the frog. (Fig. 1a).
- (11) The frog usually pauses, but may continue with burrowing.
- (12) Sequence 1 to 11 is repeated again.

These frogs tended to burrow straight down from the soil surface and would continue burrowing deeper after being covered by the substrate. They can position their digging foot in the midline of the body, and directly underneath the body. The frogs which exhibited this type of burrowing were *Notaden melanoscaphus*, *N. nichollsi* and *Neobatrachus* sp.

MYOLOGY OF THE HINDLIMB

Measurements taken of muscles in various species of the families Hylidae and Leptodactylidae are shown in Table 1. These measurements are displayed as ratios to limb length.

Descriptive myology of the hindlimb of *Cyclorana australis* is as follows:

(i) *Cyclorana australis* (Figs 2, 3, 4 and 5)

M. cruralis. Origin: by tendon from hip joint capsule between *M. iliacus internus* and *M. pectineus*. Insertion: by a broad heavy tendon inserting onto condyles of femur and onto head of tibio-fibula. Large wide muscle lying on dorso-lateral surface of thigh, separable into two parts. Anterior part approximately two-thirds as long as posterior part, and attached to posterior part by wide thin aponeurosis. Both parts originate by long thin tendons, posterior part more distally along femur.

Muscle	Ratio	C.a	SD	C.l	L.a	L.c	L.d	L.t	N.n	N.m	N.sp	L.c	L.n
C:	T:L	0.151	(0.014)	0.13	0.15	0.14	0.16	0.13	0.25	0.29	0.34	0.1	0.16
	L:Th	0.805	(0.107)	0.772	0.75	0.828	0.739	0.786	0.664	0.684	0.649	0.735	0.779
G.m.	L:Th	0.849	(0.084)	0.657	0.632	0.715	0.682	0.731	0.556	0.781	0.699	0.756	0.874
	W:L	0.204	(0.019)	0.24	0.28	0.21	0.18	0.164	0.24	0.02	0.152	0.076	0.155
G.m.n.	L:Th	0.891	(0.084)	0.868	0.909	0.996	0.932	0.720	0.755	0.899	0.827	0.924	0.893
Sm.	T:L	0.114	(0.013)	0.134	0.095	0.163	0.085	0.127	0.182	0.112	0.081	0.072	0.069
	L:Th	0.913	(0.067)	0.806	0.881	0.88	0.914	0.823	0.638	0.889	0.771	0.891	0.943
	W:L	0.238	(0.018)	0.269	0.198	0.298	0.208	0.188	0.351	0.277	0.296	0.232	0.095
G.m.j.	L:Th	0.85	(0.117)	0.803	0.922	0.921	0.941	0.729	0.741	0.845	0.773	0.882	0.893
I. fb.	L:Th	0.828	(0.061)	0.821	0.814	0.851	0.792	0.784	0.64	0.678	0.611	0.886	0.829
S.	L:Th	1.037	(0.132)	0.968	0.953	1.005	0.929	0.933	0.953	0.903	0.782	0.884	0.923
A.1.	L:Th	0.699	(0.075)	0.596	0.682	0.748	0.848	0.892	0.858	0.847	0.603	-	-
A.m.	VL:Th	0.846	(0.082)	0.865	0.838	0.885	0.916	0.831	0.826	0.818	0.766	0.83	0.911
	DW:Th	0.06	(0.009)	0.119	0.051	0.075	0.06	0.064	0.091	0.129	0.087	0.055	0.056
St.	AL:Th	0.887	(0.05)	0.937	0.895	0.943	0.898	0.86	0.813	0.87	0.667	0.85	0.932
	P:AL	0.408	(0.028)	0.478	0.574	0.453	0.608	0.713	0.625	0.7	0.705	0.582	0.337
	P:Th	0.46	(0.035)	0.447	0.514	0.427	0.547	0.613	0.508	0.609	0.47	0.495	0.362
O.e.	L:Th	0.492	(0.045)	0.532	0.473	0.388	0.531	0.345	0.394	0.502	0.464	0.447	0.278
Pc.	L:Th	0.537	(0.058)	0.533	0.537	0.61	0.584	0.339	0.718	0.761	0.523	0.506	0.480
I.f.	L:Th	0.422	(0.029)	0.365	0.403	0.362	0.43	0.425	0.23	0.287	0.279	0.358	0.240
P.1.	T:L	0.179	(0.02)	0.169	0.181	0.219	0.145	0.134	0.235	0.202	0.181	0.195	0.113
	L:TL	0.728	(0.037)	0.798	0.753	0.753	0.791	0.814	0.658	0.599	0.587	0.705	0.832
P.	L:TL	0.776	(0.024)	0.73	0.779	0.771	0.731	0.759	0.639	0.599	0.717	0.804	0.966
T.a.1.	W:TL	0.092	(0.006)	0.134	0.115	0.15	0.156	0.107	0.165	0.228	0.227	0.063	0.067
	OD:TL	0.572	(0.023)	0.594	0.6	0.604	0.589	0.728	0.175	0.309	0.292	0.557	0.729
E.c.b.	L:TL	0.556	(0.043)	0.644	0.645	0.268	0.294	0.801	0.316	0.383	0.343	0.597	0.437
	Li:L	0.876	(0.076)	0.835	0.95	0.681	0.694	0.790	0.826	0.619	0.608	0.737	0.868
T.p.	Lo:L	0.878	(0.057)	0.88	0.928	0.879	0.968	0.728	0.693	0.797	0.704	0.913	0.949
	L:TL	0.756	(0.044)	0.69	0.729	0.598	0.773	0.751	0.706	0.549	0.717	0.723	0.742
Foot	TL:S-V	0.51	(0.025)	0.405	0.46	0.46	0.385	0.446	0.35	0.335	0.35	0.453	0.735
Head	W:L	0.171	(0.009)	0.149	0.167	0.166	0.15	0.114	0.224	0.27	0.247	0.134	0.102
	L:W	0.935	(0.026)	0.941	1.015	0.833	0.903	1.075	0.727	0.989	0.737	0.866	1.373

TABLE 1. Measurements of the leg muscles and other morphological features of several frog species, expressed as ratios.

AL = anterior head length; DW = dorsal belly width; L = length; Li = length of insertion; Lo = length of origin; OD = length from origin to divergence of bellies; P = distance from origin of anterior head to insertion of posterior head; T = thickness; Th = thigh length; TL = tibia length; VL = ventral belly length; W = width; S-V = snout to vent length, SD = standard deviation, C.a. = *Cyclorana australis*; C.l. = *C. longipes*; L.a. = *Litoria albobelluata*; L.o. = *Litoria caerulea*; L.n. = *Litoria nasuta*; L.d. = *L. dumerilii*; L.t. = *L. tamaritensis*; N.m. = *N. melanoscaphus*; N.sp. = *Neobatrachus* sp.; L.c. = *Litoria caerulea*; L.n. = *Litoria nasuta*; M. = *M. cruralis*; G.m. = *M. glutaeus magnus*; G.m.n. = *M. gracilis minor*; Sm. = *M. semimembranosus*; G.m. = *M. gracilis major*; 1fb. = *M. ilio-fibularis*; S. = *M. sartorius*; A.m. = *M. adductor longus*; A.m. = *M. adductor magnus*; St. = *M. semitendinosus*; O.e. = *M. obliquo externus*; Pc. = *M. pectineus*; Li. = *M. ilio-femoralis*; P.l. = *M. plantaris longus*; P. = *M. peroneus*; T.a.1. = *M. tibialis anticus longus*; E.c.b. = *M. extensor cruris brevis*; T.p. = *M. tibialis posticus brevis*.

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M. glutaeus magnus. Origin: from dorso-lateral border of ilium by short flat tendon. Insertion: by long broad thin aponeurosis which fuses with aponeurosis of *M. cruralis*, covering knee. Large flattened muscle lying close to *M. cruralis*. Fleishy for approximately four-fifths of length and exchanges some fibres with *M. cruralis*. Accessory tendon present arising from fascia covering sacral region and fusing with tendon of origin.

M. gracilis minor. Origin: from ischiac region of pelvic rim just ventral to anus by short, flat, thin tendon. Insertion: unites on distal extremity with *M. gracilis major* forming a common tendon inserting under *M. sartorius* to ventro-lateral side of aponeurosis covering knee. Also inserts by second long tendon onto tibio-fibula just below head on dorso-medial side, just near origin of *M. plantaris longus*. Very thin, wide muscle, covering all of *M. gracilis major* dorsally and about one-third of mass ventrally. Lightly attached to skin; muscles on both legs attached to each other at their origins.

M. tensor fasciae latae. Origin: by broad tendon from ventro-lateral surface of ilium, just posterior to centre. Insertion: by long flat very thin tendon onto proximal third of *M. cruralis*, very close to *M. glutaeus magnus*, on the dorso-lateral surface of thigh. Long thin muscle, wider at insertion than origin.

M. semimembranosus. Origin: fleshy, from ventro-lateral surface of ischium, ventral to anus. Insertion: by short tendon inserting on distal medio-ventral femur and head of tibio-fibula. *M. gracilis minor* covers origin of muscle and *M. plantaris longus* covers insertion. Muscle fairly thick, *M. ileo-fibularis*, *M. plantaris longus* and *M. gracilis major* all connected to it near its insertion.

M. gracilis major. Origin: from postero-ventral pelvic rim by broad, short tendon, slightly ventral to origin of *M. gracilis minor*. Insertion: by two tendons, one broad inserts on tendon covering knee and one long tendon which lies between tendon of *M. semitendinosus* and *M. semimembranosus* inserting onto tibio-fibula on its dorsal-medial side. Broad, slightly flattened muscle lying along medio-ventral thigh.

M. ileo-fibularis. Origin: from postero-ventral border of ilium by short, slender tendon. Insertion: into aponeurosis covering knee by one long, slender tendon. Insertion covered by one tendon of origin of *M. plantaris longus*. Long muscle lying on dorsal surface of thigh, and flattened anteroposteriorly.

M. adductor longus. Origin: by short tendon from iliac portion of ventral pelvic rim and dorsal to origin of *M. sartorius*. Insertion: fleshy onto lateral face of *M. adductor magnus*.

M. sartorius. Origin: from antero-lateral border of ventral pelvic rim and from ventral surface of *M. adductor longus* by a very short, thin tendon. Insertion: by narrow, flat tendon that bifurcates and attaches anteriorly to aponeurosis covering knee, and posteriorly to ventral surface of tibio-fibula. Also attached anteriorly to tendon of insertion of *M. gracilis major* and *M. semitendinosus*. Long, flat, thin muscle that twists around thigh from latero-anterior to medio-posterior surface.

M. adductor magnus. Origin: by two heads. Large ventral head arises from ventral border of pelvic rim by wide, short tendon. Dorsal head arises with fleshy origin from pelvic rim beneath *M. gracilis minor*, from ventro-posterior pelvic rim between two origins of *M. semitendinosus*. Insertion: ventral belly fuses with an accessory head arising from *M. semitendinosus* and inserting along medio-ventral border of distal part of femur. Smaller dorsal belly fuses with ventral and accessory heads and inserts along distal half of dorsal and dorso-lateral femur. Accessory head of medium size and inserts around most of distal end of femur. Ventral head larger and thicker than dorsal head and receives insertion of *M. adductor longus*.

M. semitendinosus. Origin: by two heads. Anterior head arises by very long, thin tendon from postero-ventral pelvic rim, ventral to *M. quadratus femoris* and anterior to origin of dorsal head of *M. adductor magnus*. Posterior head arises with fleshy origin from postero-dorsal pelvic rim, just posterior to *M. semimembranosus*. Insertion: anterior head inserts by long, narrow tendon onto ventral surface of tibio-fibula, joining with *M. sartorius*. Posterior head inserts onto anterior head and a tendon continues to insertion at knee. Muscle of two parts which share a common tendon of insertion. It lies on ventral and posterior part of thigh, with both heads being separated by *M. quadratus femoris*.

M. quadratus femoris. Origin: fleshy, from ventro-posterior pelvic rim just posterior to *M. obturator externus*, and separated from it by a tendon of *M. semitendinosus*. Insertion: fleshy and with many small tendons on ventro-medial surface of femur in proximal half. Short,

triangular muscle lying very close and anterior to *M. gemellus* and sometimes difficult to separate from it. It also may be difficult to separate from *M. obturator externus*.

M. obturator externus. Origin: fleshy, from ventro-lateral surface of pelvic rim. Insertion: fleshy on proximal half of ventral surface of femur, medial to insertion of *M. pectineus*. Muscle thick, slightly triangular shaped with wide origin. Short attachment to *M. quadratus femoris*.

M. pectineus. Origin: fleshy, from anterior pelvic rim, anterior to *M. obturator externus*, and deeper than *M. sartorius*. Insertion: fleshy on ventral surface of proximal half of femur. Muscle has wide origin and tends to be flattened in antero-posterior plane. Approximately same length as *M. obturator externus*.

M. iliacus internus. Origin: fleshy, from medial and ventral border of ilium. Insertion: broad fleshy insertion on dorsal, medial and lateral aspects of femur on proximal two-thirds of bone. Large dorso-ventrally flattened muscle of wide origin with insertion covering large area of femur.

M. gemellus. Origin: fleshy, from posterior pelvic rim, posterior to *M. quadratus femoris*. Insertion: fleshy onto dorso-medial aspect of proximal half of femur. Short, triangular shaped muscle overlain by *M. quadratus femoris* and *M. pyramidalis*, in some specimens.

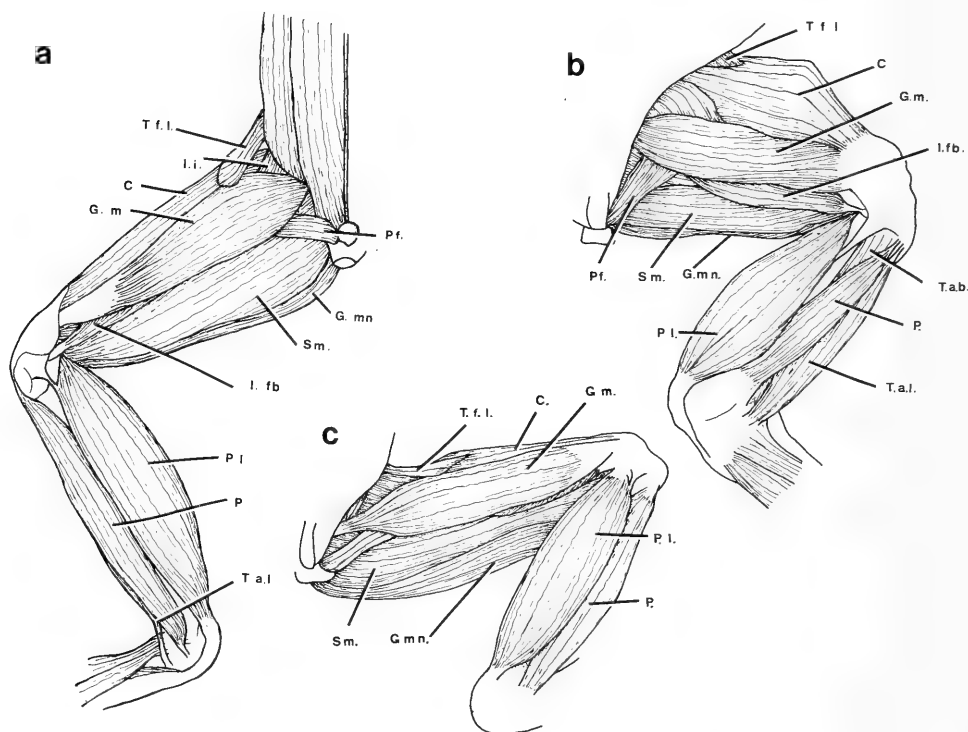


Fig. 2. Dorsal view of superficial musculature of the leg of (a) *Cyclorana australis*, (b) *Notaden nichollsi* and (c) *Litoria caerulea*. T.f.l. *M. tensor fasciae latae*; I.i. *M. iliacus internus*; C. *M. cruralis*; G.m. *M. glutaeus magnus*; Pf. *M. pyramidalis*; G.mn. *M. gracilis minor*; S.m. *M. semimembranosus*; I.fb. *M. ileo-fibularis*; P.l. *M. plantaris longus*; P. *M. plantaris brevis*; T.a.l. *M. tibialis anticus longus*; T.a.b. *M. tibialis anticus brevis*.

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M. pyriformis. Origin: fleshy, from dorso-lateral border of distal end of coccyx. Insertion: fleshy, on dorso-medial surface of femur, between *M. quadratus femoris* and *M. ileo-femoralis*. Long, flattened muscle of dorsal surface in which insertion overlays *M. gemellus*.

M. iliacus externus. Origin: fleshy, from lateral, dorsal and medial surfaces of the ilium from about halfway down. Insertion: by large broad tendon onto dorso-medial surface of femur, passing just dorsal to *M. ileo-femoralis*. Large, almost spindle shaped muscle lying on dorsal surface. Area of origin varies and may consist of two heads, one medial and the other dorso-lateral.

M. ileo-femoralis. Origin: partly fleshy from postero-ventral surface of ilium ventral to origin of *M. ileo-fibularis* and in part from tendon of origin of *M. ileo-fibularis*. Insertion: wide and fleshy, along proximal third of dorso-medial border of femur between *M. pyriformis* and *M. iliacus internus*, but extending beyond *M. pyriformis*. Deep muscle of dorsal surface, dorso-ventrally flattened. Point of insertion ends more proximally on femur than in *M. iliacus internus*.

M. plantaris longus. Origin: by two tendinous heads, one short, thick tendon from medial border of knee joint, one long, thin tendon from dorso-distal border of tendon covering knee. Insertion: thick flattened tendon forms an aponeurosis covering plantar surface of foot. Large almost cylindrical muscle lying along medial surface of tibia-fibula for bone's entire length. *M. ileo-fibularis* dorsal to large tendon of origin, but inserts ventral to thin tendon of origin.

M. peroneus. Origin: from a short heavy ligament on extensor surface of knee joint, with a long tendon passing underneath aponeurosis covering knee. Insertion: by a short tendon onto distal end of dorsal surface of tibio-fibula proximal to *M. tibialis anticus longus*. Large flattened muscle covering most of dorsal-lateral surface of tibio-fibula.

M. tibialis anticus longus. Origin: from latero-ventral surface of median condyle of femur, a long tendon passes over a groove in lateral surface of tibio-fibula and penetrates tendon of *M. peroneus*. Insertion: by two tendinous heads, one onto dorso-lateral surface of proximal end of fibula, other on ventro-lateral surface of proximal end of tibia. Covers lateral surface of shank and diverges into two bellies for distal half. In most specimens ventral belly less fleshy and not as thick as dorsal belly.

M. tibialis anticus brevis. Origin: fleshy, from middle third of tibio-fibula dorsal to *M. extensor cruris brevis*. Insertion: by short tendon on proximo-ventral surface of tibio-fibula just dorsal to ventral belly of *M. tibialis anticus longus*. Small muscle with very wide fleshy origin. Passes medial to *M. tibialis anticus longus* in passing from dorsal to ventral surface of tibio-fibula.

M. extensor cruris brevis. Origin: from long tendon from ventral surface of medial condyle of femur, passes over extensor surface of knee. Insertion: fleshy, along latero-ventral surface of tibio-fibula for most of length. Long, narrow muscle that for most of length inserts on tibio-fibula, between *M. tibialis anticus brevis* and *M. tibialis posticus brevis*.

M. tibialis posticus brevis. Origin: fleshy, from entire medial surface of shaft of tibio-fibula. Insertion: by long tendon extending around distal end of tibio-fibula medio-ventrally, onto tibio-fibula proximal to ventral head of *M. tibialis anticus longus*. Long, slender muscle with very long origin. Lies medially on tibio-fibula just deeper than *M. plantaris longus*, with insertion covered by plantar aponeurosis of *M. plantaris longus*.

Descriptive myology of the following species of frogs examined includes only those features that differ from the condition shown by *Cyclorana australis*.

(ii) *Cyclorana longipes*

M. gluteus magnus. Muscle narrow at its origin, slightly rounded on dorsal surface. Fleshy for approximately three-quarters of length lying very close to *M. cruralis*, exchanging fibres with it.

M. gracilis minor. Origin: tendon narrower. Lies on medial and ventro-medial surfaces of thigh. Attached to skin and covers *M. gracilis major* on its medial surface. Head of origin thick.

M. tensor fasciae latae. Insertion: on lateral aspect of thigh. Muscle does not insert as close to *M. gluteus magnus*.

M. gracilis major. Origin: by short, narrow tendon from postero-ventral pelvic rim. Ventral and adjacent to origin of *M. semimembranosus*. Large thick muscle lying on ventro-medial aspect of thigh. Can be divided into two almost equal bellies.

M. ileo-fibularis. Long spindle-shaped muscle lying on dorsal surface of thigh, partially obscured by *M. gluteus magnus*.

M. sartorius. Origin: in one specimen muscle had a second point of origin further ventrally, along pelvic rim. Muscle lies on ventral surface of thigh. Second origin resulted in a long bifurcation of muscle.

M. adductor longus. Insertion: fleshy, on latero-ventral face of *M. adductor magnus* in distal third of that muscle.

M. adductor magnus. Insertion: smaller dorsal head extends to medial femur at insertion.

M. semitendinosus. Muscle with two heads lying on ventral and posterior aspects of thigh.

M. quadratus femoris. Origin: fleshy, from ventral to ventro-posterior pelvic rim. Insertion: along proximal third of ventro-posterior to posterior femur. Very wide origin, fused to *M. obturator externus* in some specimens.

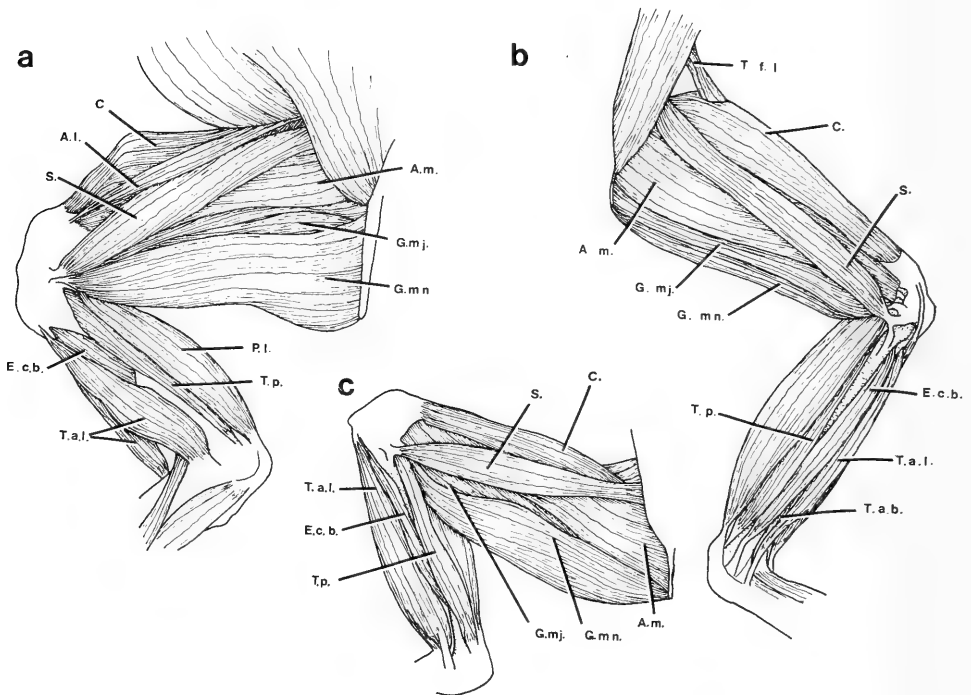


Fig. 3. Ventral view of superficial musculature of the leg of (a) *Notaden nicholli* (b) *Cyclorana australis* and (c) *Litoria caerulea*. C. *M. cruralis*; A.l. *M. adductor longus*; S. *M. sartorius*; E.c.b. *M. extensor brevis*; T.a.l. *M. tibialis anticus longus*; A.m. *M. adductor magnus*; G.mj. *M. gracilis major*; G.mn. *M. gracilis minor*; P.l. *M. plantaris longus*; T.p. *M. tibialis posticus brevis*; T.f.l. *M. tensor fasciae latae*; T.a.b. *M. tibialis anticus brevis*.

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M. obturator externus. Origin: fleshy from ventral to ventro-posterior pelvic rim. Short muscle of wide origin, approximately same length as *M. pectineus*.

M. pectineus. Origin and insertion: fleshy, lying just anterior to *M. obturator externus*.

M. iliacus internus. Insertion: inserts on proximal half of femur.

M. gemellus. Insertion: onto medial femur near head of bone. Insertion overlain by *M. quadratus femoris*. Small, triangular-shaped muscle almost hidden by larger *M. quadratus femoris*. Lies on medial proximal femur with a more medial insertion than *M. quadratus femoris* or *M. pyriformis*.

M. pyriformis. Insertion: on proximal, medial femur between *M. gemellus* and *M. ileo-femoralis*. Long, cylindrical-shaped muscle flattened at its insertion and lying on dorsal surface of femur.

M. iliacus externus. Origin: by two heads, one from a large flat tendon and one fleshy. Originates from dorsal, lateral and medial sides of ilium approximately half way down. Large, spindle-shaped muscle.

M. ileo-femoralis. Insertion: fleshy in proximal third of medial femur. Insertion extends beyond *M. pyriformis*. Dorso-ventrally flattened muscle of dorsal thigh.

M. plantaris longus. Large muscle lying on medial surface of shank, rounded on its medial surface and flattened on surface lying against shank.

M. peroneus. Large muscle lying on dorsal shank, overlain in part by *M. plantaris longus*. Muscle very wide at insertion.

M. tibialis anticus longus. Muscle lying along lateral aspect of shank. Split into two bellies in its distal half, with dorsal belly being more fleshy than ventral belly.

M. tibialis anticus brevis. Origin: fleshy, from middle of dorsal tibio-fibula, dorsal to *M. extensor cruris brevis*. Insertion: dorsal to that of *M. tibialis anticus longus*.

(iii) *Litoria alboguttata*

M. cruralis. Large, broad muscle lying slightly more toward ventro-lateral aspect of thigh.

M. gluteus magnus. Origin: very short wide tendon. Large muscle dorso-ventrally compressed and lying close to *M. cruralis* exchanging some fibres with it. Slightly concave near insertion.

M. gracilis minor. Wide, flat, thin muscle lightly attached to skin. Both muscles are lightly joined at origins.

M. tensor fasciae latae. Insertion: inserts more onto *M. cruralis* dorso-ventral aspect. Long, thin muscle, but slightly thicker than in *C. australis*.

M. semimembranosus. Origin: two fleshy heads. Small head lies ventral and more posterior to larger dorsal head. Two heads of muscle can be separated to muscle insertion.

M. gracilis major. Origin: tendon narrow, and head of belly thickened.

M. quadratus femoris. Origin: from dorso-posterior pelvic rim. Insertion: along dorso-medial femur in its proximal half. Short muscle, rectangular shaped and lying slightly more dorsally.

M. obturator externus. Origin: from ventral to ventro-posterior pelvic rim. Insertion: fleshy, along proximal half of ventro-posterior aspect of femur, proximal to insertion of *M. pectineus*.

M. pectineus. Inserts more distally than *M. obturator externus*.

M. gemellus. Origin: from dorso-posterior pelvic rim. Small, triangular-shaped muscle, shorter than *M. quadratus femoris* but wider at its origin.

M. pyriformis. Insertion: slightly more dorsal.

M. iliacus externus. Origin: sometimes consists of two heads. Insertion: tendon more cylindrical in shape.

M. peroneus. Large muscle completely covers *M. tibialis anticus longus* on dorsal tibio-fibula.

M. tibialis anticus longus. Ventral belly fleshy for only a small part of its length.

M. tibialis anticus brevis. Origin: from distal third of dorsal to dorso-lateral tibio-fibula.

M. tibialis posticus brevis. Origin: extends slightly more dorsally and ventrally.

(iv) *Limnodynastes ornatus*

M. cruralis. Origin: tendon of posterior head thicker, muscle wider at origin. Muscle slightly wider and slightly concave on dorso-lateral surface.

M. gluteus magnus. Insertion: short tendon. Muscle slightly rounded, fleshy for a greater proportion of length. Accessory tendon present.

M. gracilis minor. Origin: tendon wider and thinner. Can be separated into two flat heads of different widths. Insertion: by one short tendon to aponeurosis covering knee. Much wider muscle extending more onto ventral surface of thigh and covering *M. gracilis major*.

M. gracilis major. Insertion: by one long tendon only, onto aponeurosis covering knee, passing dorsal to *M. sartorius*.

M. ileo-fibularis. Origin: tendon broader.

M. adductor longus. Insertion: fleshy on distal third of *M. adductor magnus*.

M. obturator externus. Origin: extending more anteriorly along pelvic rim. Insertion: on proximal third of ventro-posterior femur, just proximal to *M. pectineus*.

M. pectineus. Origin: from antero-ventral to anterior pelvic rim. Insertion: along middle of ventro-posterior femur, and extends distally to *M. obturator externus*.

M. iliacus internus. Insertion: extends more ventrally.

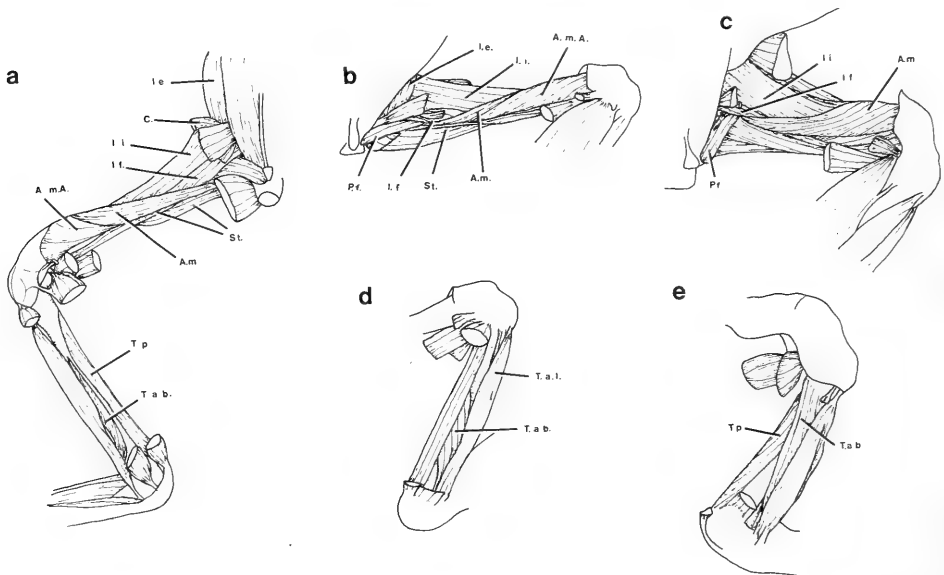


Fig. 4. Dorsal view of deep musculature of (a) thigh and shank of *Cyclorana australis*, (b) thigh of *Litoria caerulea*, (c) thigh of *Notaden nichollii*, (d) shank of *Litoria caerulea*, (e) shank of *Notaden nichollii*. I.e. *M. iliacus externus*; C. *M. cruralis*; I.i. *M. iliacus internus*; A.m.A. *M. adductor magnus*, accessory head; St. *M. semi-tendinosus*; A.m. *M. adductor magnus*; T.p. *M. tibialis posticus brevis*; T.a.b. *M. tibialis anticus brevis*; Pf. *M. pyriformis*; T.a.l. *M. tibialis anticus longus*. I.f. *M. ileo-femoralis*.

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M. gemellus. Origin: slightly more dorsal. Muscle larger than *M. quadratus femoris*.

M. iliacus externus. Origin: from one head.

M. tibialis anticus longus. Origin: tendon wider. Ventral belly, although less fleshy, wider than dorsal belly.

M. tibialis anticus brevis. Origin: from proximal half of ventro-lateral and dorso-lateral tibia, distal and ventral to *M. extensor cruris brevis*. Insertion: by large rounded tendon and just proximal to *M. tibialis anticus longus*. Larger, thicker muscle and with different origin.

M. extensor cruris brevis. Insertion: more lateral extending only halfway down shank. Very short muscle overlain distally by *M. tibialis anticus brevis*.

M. tibialis posticus brevis. Origin: from medial to medio-ventral tibio-fibula, in distal two-thirds. Muscle very thin at its proximal end but thickens and becomes rounded closer to its insertion.

(v) *Limnodynastes dumerili*

M. cruralis. Origin: thicker. Both heads almost same length. Muscle not as broad.

M. gluteus magnus. Insertion: tendon much shorter. Muscle fleshy almost to insertion. Accessory tendon large, flat.

M. gracilis minor. Origin: from short, very wide tendon extending from pelvic rim just ventral to anus. Muscle divided into two portions, one thick and pointed, and other wide and flat.

M. ileo-fibularis. Origin: tendon longer.

M. adductor longus. Insertion: fleshy onto *M. adductor magnus* near its insertion.

M. adductor magnus. Insertion: dorsal belly inserts more distally on femur.

M. semitendinosus. Insertion: posterior head larger and inserts on distal half of anterior head.

M. quadratus femoris. Only slightly fused to *M. obturator externus*.

M. iliacus internus. Insertion: extends into distal half of femur.

M. gemellus. Origin: from dorso-posterior pelvic rim, dorsal to *M. quadratus femoris*. Insertion: more medial, approximately as far distal as that of *M. quadratus femoris*.

M. pyriformis. Insertion: on femur in middle but dorsal to insertion of *M. ileo-femoralis*.

M. peroneus. Large flattened muscle partially overlying *M. tibialis anticus longus*.

M. tibialis anticus longus. Origin: tendon larger and flatter.

M. tibialis anticus brevis. Origin: from middle third of dorso-lateral and lateral tibio-fibula, immediately distal and ventral to insertion of *M. extensor cruris brevis*. Insertion: dorsal to that of *M. tibialis anticus longus*.

M. extensor cruris brevis. Insertion: fleshy along dorso-ventral tibia, proximal to origin of *M. tibialis anticus brevis*.

M. tibialis posticus brevis. Origin: extends more ventrally.

(vi) *Limnodynastes tasmaniensis*

M. gluteus magnus. Wide accessory tendon.

M. gracilis minor. Very small and narrow; lies on surface of *M. gracilis major*. Attached to skin.

M. tensor fasciae latae. Origin: from anterior dorso-lateral ilium. Very long muscle.

M. adductor longus. Insertion: on *M. adductor magnus* near its insertion and also on knee. Large muscle.

M. semitendinosus. Posterior head inserts on distal half of anterior head.

M. quadratus femoris. Insertion: at same point as *M. obturator externus* and *M. gemellus*.

M. obturator externus. Insertion: proximal half of femur; same length as *M. pectineus*.

M. gemellus. Same shape and length as *M. quadratus femoris*.

M. ileo-femoralis. Extends beyond *M. pyriformis*.

M. plantaris longus. Fleishy portion short.

M. tibialis anticus longus. Both heads fleshy, dorsal head slightly thinner.

M. tibialis anticus brevis. Very small muscle.

(vii) *Litoria caerulea* (Figs 2, 3, 4 and 5)

M. cruralis. Much smaller, thinner muscle.

M. gluteus magnus. No accessory tendon present.

M. semimembranosus. Origin: wide, short tendon from dorso-posterior and posterior pelvic rim. Two heads can be separated.

M. sartorius. Origin: long, thin tendon.

M. adductor longus. Absent.

M. obturator externus. Insertion: just shorter than *M. pectineus*.

M. iliacus internus. Insertion: more ventral.

M. gemellus. Origin: fleshy, from dorso-posterior pelvic rim, just under anus. Insertion: fleshy on medial femur terminating well short of that of *M. ileo-femoralis*. Same length as *M. quadratus femoris*.

M. peroneus. Insertion: tendon shorter and wider.

M. tibialis anticus longus. Insertion: ventral head very short.

M. tibialis anticus brevis. Insertion: distal and dorsal to *M. extensor cruris brevis*.

M. extensor cruris brevis. Insertion: inserts on only three-quarters of proximal tibio-fibula.

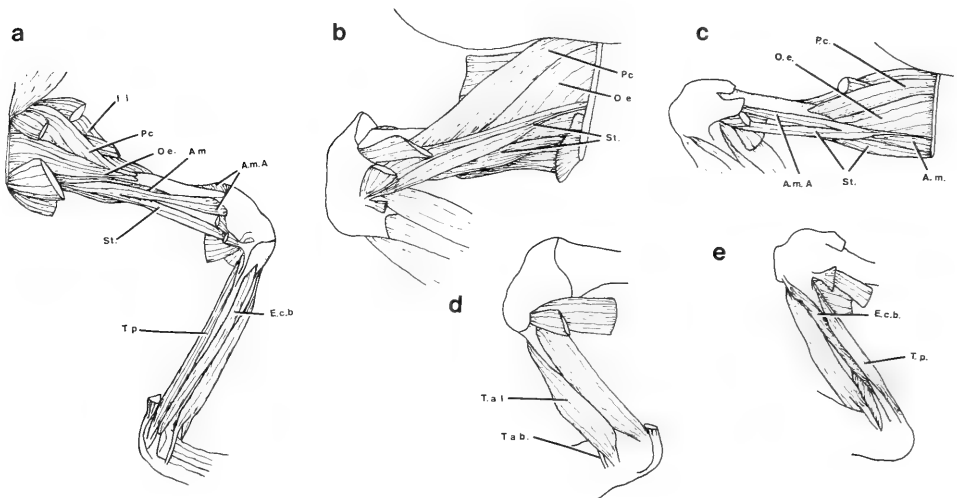


Fig. 5. Ventral view of the deep musculature of (a) thigh and shank of *Cyclorana australis*, (b) thigh of *Notaden nichollsi*, (c) thigh of *Litoria caerulea*, (d) shank of *Notaden nichollsi*, (e) shank of *Litoria caerulea*. I.i. *M. iliacus internus*; Pc. *M. pectineus*; O.e. *M. obturator externus*; A.m. *M. adductor magnus*; Am.A. *M. adductor magnus*, accessory head; St. *M. semitendinosus*; T.p. *M. tibialis posticus brevis*; E.c.b. *M. extensor cruris brevis*; T.a.l. *M. tibialis anticus longus*; T.a.b. *M. tibialis anticus brevis*.

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(viii) *Litoria nasuta*

M. cruralis. Muscle not very wide, interchange of fibres with *M. glutaeus magnus*. Anterior head shorter than posterior head. Posterior head with narrow origin.

M. glutaeus magnus. Exchanges fibres with *M. cruralis*. Origin: with wide, thin accessory tendon. Insertion: by flat thin tendon.

M. gracilis minor. Origin: from posterior pelvic rim. Muscle fused to *M. gracilis major*.

M. tensor fasciae latae. Insertion: near origin of *M. cruralis*.

M. semimembranosus. Origin: fleshy from postero-dorsal pelvic rim.

M. ileo-fibularis. Origin: by long tendon from tip of ilium.

M. sartorius. Origin: from anterior pelvic rim only.

M. adductor longus. Absent.

M. semitendinosus. Posterior head inserts on distal half of anterior head.

M. quadratus femoris. Origin: from posterior pelvic rim. Insertion: on medial femur between *M. gemellus* and *M. obturator externus*. Very small muscle, shorter than *M. gemellus*.

M. obturator externus. Origin: from ventral pelvic rim. Insertion: ventral to ventro-medial femur in proximal half. Muscle fused to *M. quadratus femoris* and *M. pectineus*; shorter than *M. pectineus*.

M. pectineus. Origin: from antero-ventral pelvic rim. Insertion: along ventral femur. Muscle longer than *M. obturator externus*.

M. iliacus externus. Origin: by one fleshy head from dorsal, lateral and ventral ilium.

M. tibialis anticus longus. Origin: from very long tendon. Long narrow muscle with ventral belly less bulky than dorsal belly.

(ix) *Notaden nichollsi* (Figs 2, 3, 4 and 5)

M. cruralis. Origin: two portions have thicker origins and are very close together. Muscle very wide, short and thick, lateral surface concave with deep furrows distally. Both portions almost of equal length.

M. glutaeus magnus. Origin: tendon short and cylindrical. Insertion: by very short, wide tendon onto aponeurosis covering knee. Thick cylindrical muscle that does not lie close to *M. cruralis* except at distal end. Exchanges some fibres with *M. cruralis*, fleshy all the way to its insertion. No accessory tendon present.

M. gracilis minor. Origin: tendon wider. Muscle divided into two sheets close to origin. Insertion: only by one short tendon onto the aponeurosis covering knee. Very wide muscle at its origin, extending mostly onto ventral surface of thigh, covering *M. gracilis major*.

M. tensor fasciae latae. Insertion: fleshy, on *M. cruralis*, approximately halfway down. Muscle very small and thin, but longer.

M. semimembranosus. Origin: slightly more medial. Insertion: more ventral. Muscle can be split into two heads, large dorsal and smaller ventral head which arises from posterior pelvic rim.

M. gracilis major. Origin: from postero-ventral to ventral pelvic rim, by very short, wide, thin tendon. Insertion: by one tendon only, under aponeurosis of *M. sartorius*. Wide origin of this muscle gives it triangular shape.

M. ileo-fibularis. Larger, slightly more rounded muscle.

M. adductor longus. Insertion: onto *M. adductor magnus* near insertion, by a tendon onto ventro-lateral surface of aponeurosis covering knee, just ventral to *M. cruralis*. Muscle longer and larger. Not covered by *M. sartorius*, but lies anterior to it.

M. adductor magnus. Origin: ventral head arises anteriorly to the origin of *M. semitendinosus*. Insertion: ventral head inserts more towards the lateral femur.

M. semitendinosus. Insertion: posterior head inserts more distally on anterior head.

M. quadratus femoris. Origin: slightly more posterior.

M. obturator externus. Origin: extends more anteriorly. Insertion: proximal to insertion of *M. pectineus*.

M. pectineus. Origin: extends more anteriorly. Insertion: fleshy, on ventro-posterior femur, extending past *M. obturator externus*, to distal half of femur.

M. iliacus internus. Insertion: extends into distal half of femur.

M. gemellus. Insertion: fleshy, onto medial femur in between *M. quadratus femoris* and *M. pyramidalis*.

M. iliacus externus. Origin: sometimes has only one head.

M. ileo-femoralis. Insertion: does not extend beyond insertion of *M. pyramidalis*.

M. peroneus. Insertion: more medial to insertion of *M. tibialis anticus longus*. Does not overlap *M. tibialis anticus longus* completely.

M. tibialis anticus longus. Origin: from wide, flat tendon. Insertion: more distal. Two bellies of equal length, but ventral belly much wider than dorsal. Very large divergence between bellies which are split almost to origin. Muscle much thicker and wider.

M. tibialis anticus brevis. Origin: from proximal half of dorso-medial to lateral tibio-fibula. Insertion: more distal to *M. tibialis anticus longus* by a long tendon. Muscle much longer and wider.

M. extensor cruris brevis. Insertion: on proximal half of ventro-lateral tibio-fibula. Muscle much smaller.

M. tibialis posticus brevis. Origin: from medial to medio-ventral tibia, for almost whole of its length. Two heads of origin, one in dorso-medial to medial region, other in ventro-medial region.

Descriptive myology of the remaining species of frogs includes only those features that differ from those of *Notaden nichollsi*.

(x) *Notaden melanoscaphus*

M. gracilis minor. Origin: two rounded heads, attached by tendons to pelvic rim, each other, and to *M. gracilis minor* of other leg. Strongly attached to skin at origin.

M. adductor longus. Origin: immediately dorsal to *M. sartorius*. Insertion: by tendon onto ventro-lateral tendon covering knee. Does not insert on *M. adductor magnus*.

M. adductor magnus. Origin: more anterior origin for both heads, and they do not cover *M. semitendinosus*. Insertion: dorsal head much wider and extends more distally.

M. obturator externus. Origin: more anterior.

M. pectineus. Insertion: extends to distal end of femur.

M. iliacus internus. Insertion: from medio-ventral to latero-dorsal femur and extends into distal half.

M. gemellus. Origin: from dorso-posterior pelvic rim. Insertion: fleshy on medial femur overlying shorter *M. quadratus femoris*.

M. ileo-femoralis. Insertion: is covered by *M. pyramidalis* and does not extend beyond it.

M. extensor cruris brevis. Origin: tendon long and broad.

M. tibialis posticus brevis. Origin: wider.

(xi) *Neobatrachus* sp.

M. cruralis. Large, thick, humped muscle very similar to *N. nichollsi*.

M. gluteus magnus. Origin: by short, thick tendon.

M. gracilis minor. Origin: by wide, short, thin tendon from postero-dorsal pelvic rim. Very wide muscle, extending more onto ventral surface, and covering *M. gracilis major*.

M. gracilis major. Origin: by short, wide tendon from ventro-posterior pelvic rim.

M. ileo-fibularis. Origin: as in *C. australis*, but by long, stout tendon. A long, cylindrical muscle, thicker than in *C. australis*.

M. adductor longus. Insertion: fleshy, on *M. adductor magnus* near its insertion.

M. quadratus femoris. Origin: as in *C. australis*, but more posterior.

M. obturator externus. Insertion: as in *C. australis*. Muscle almost as long as *M. pectineus*.

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M. gemellus. Origin: fleshy, from dorso-posterior pelvic rim. Insertion: as in *C. australis*, but more medial.

M. pyriformis. Insertion: on medial femur in middle of *M. ileo-femoralis*.

M. peroneus. Origin: as in *C. australis*, but more dorsal.

M. tibialis posticus brevis. Origin: medio-dorsal head shorter and more separate.

DISCUSSION

This study examined a number of frogs from the families Hylidae and Leptodactylidae, with respect to burrowing behaviour and hindlimb myology. Some systematic differences were found within the hindlimb myology of representatives of the two families. Within the leptodactylid species:

- (1) origins of *M. cruralis* tended to be thicker with the anterior head of the muscle larger,
- (2) *M. glutaesus magnus* tended to be more fleshy distally,
- (3) origin of *M. gracilis minor* from two separate heads, was wider,
- (4) insertion of *M. gracilis major* was by one less tendon (except in *Limnodynastes dumerili*),
- (5) *M. adductor longus* tended to be longer,
- (6) *M. obturator externus* and *M. pectineus* had wider origins,
- (7) origin of *M. tibialis anticus brevis* was more proximal (except in *Limnodynastes dumerili*),
- (8) *M. extensor cruris brevis* tended to be shorter,
- (9) *M. tibialis posticus* tended to be wider,

than in hylid species. Dunlap (1960) reported the accessory tendon of the *M. glutaesus magnus* to be absent in the Hylidae; however, in this study it was found to be present in some species of both the Hylidae and Leptodactylidae. *M. gracilis minor* was attached to the skin in varying degrees in all the frogs studied here, not only in leptodactylids as reported by Dunlap (1960).

Many of the similarities of thigh musculature between the frogs examined may be adaptations to the burrowing habit. For this reason a non-burrowing leptodactylid, *Limnodynastes tasmaniensis* and two non-burrowing hylids, *Litoria caerulea*, a tree-dwelling species and *L. nasuta*, a ground dwelling species, were examined. The non-burrowing hylids differed from the burrowing hylids in the following respects:

- (1) *M. adductor longus* was absent,
- (2) *M. tibialis anticus longus* was narrower,
- (3) *M. cruralis* was narrower.

One might infer from these data that presence of *M. adductor longus* is associated with the burrowing habit. However, *Litoria dablii*, a non-burrowing

hylid species closely related to the burrowing hylids examined in this study and lacking the fossorial adaptations exhibited by other burrowing hylids, possesses a *M. adductor longus* of similar nature to that of the fossorial *L. alboguttata* (T. C. Burton, pers. comm.). Hence the inference is not supported.

The non-burrowing *Limnodynastes tasmaniensis* differed from the burrowing leptodactylids in that the *M. tibialis anticus longus* was narrower.

Thus it can be seen that between the burrowing and non-burrowing representatives of each family, the consistent myological difference found was in the relative width of the *M. tibialis anticus longus*. This muscle is a flexor of the ankle joint and extensor of the tibio-fibula (Calow & Alexander, 1973; Emerson, 1976). The increase in size of *M. tibialis anticus longus* would increase the force of lower leg extension at the knee, without involving movement of the hip (Emerson, 1976) which would be an aid to backwards burrowing. An increase in the mass of this muscle is seen in many burrowing frogs (Dunlap, 1960).

The differences in musculature between families are not as striking, however, as those related to different methods of burrowing. Behaviourally two different kinds of burrowing were observed. The 'backward sliding' burrowers are found in both the hylids and leptodactylids, whereas the 'circular burrowers' have representatives only amongst the Leptodactylidae.

Within the backwards sliding burrowers the following interfamilial differences in hindlimb myology were observed. Within the Leptodactylidae:

- (1) *M. extensor cruris brevis* is much shorter,
- (2) *M. gracilis minor* has a wider origin with two heads,
- (3) *M. adductor longus* is longer,
- (4) *M. iliacus externus* inserts more proximally,

than in the Hylidae.

A comparison of the 'circular' burrowing species *Notaden nichollsi*, *N. melanoscaphus* and *Neobatrachus* sp. with the backwards sliding species *Limnodynastes ornatus* and *L. dumerili* within the Leptodactylidae reveals the following striking differences. In the circular burrowers:

- (1) *M. cruralis* is humped and thicker and tends to be shorter,
- (2) *M. tibialis anticus longus* is wider with a more proximal divergence between the heads and a more distal insertion. Both of the heads are of the same length but the ventral head is wider than the dorsal,
- (3) *M. tibialis anticus brevis* has a more proximal origin which has also been shifted medially, and a more distal insertion,
- (4) *M. extensor cruris brevis* is much shorter,
- (5) *M. tibialis posticus brevis* has a wider origin which can be divided into two heads,

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- (6) *M. tensor fasciae latae* inserts more distally,
 - (7) *M. gracilis minor* has a wider origin,
 - (8) *M. adductor longus* inserts on or nearer to the knee,
 - (9) *M. pectineus* and *M. iliacus internus* insert more distally,
 - (10) the posterior head of *M. semitendinosus* inserts more distally,
- than in the backwards sliding burrowers.

The first five of these differences relate to the muscles associated with the tibio-fibula and it would seem that the major difference between the circular and non-circular burrowers is an increase in the mass of the muscles of the lower leg. Table 1 quantifies most of these differences. The shift in origin of *M. tibialis anticus brevis* lengthens this muscle. Since *M. tibialis anticus brevis* is responsible for bringing the metatarsal tubercle into position by inversion of the foot, the velocity of contraction of the muscle would be increased thus increasing efficiency (Abbott & Wilkie, 1953). The more distal insertion of this muscle on the foot may also allow a greater degree of inversion of the foot.

The increase in width of *M. cruralis* and its origins may allow more force in knee extension and the more distal insertion of *M. pectineus* and *M. iliacus externus* enables the hindlimb to be retracted and protracted to a greater extent.

The myological differences between 'circular' burrowers and 'backwards sliding' burrowers are associated with shorter limbs, small heads and globose bodies. In two of the three species the metatarsal tubercle is keratinized. In jumping frogs, the greater mass of muscle tends to be located on the thigh (Emerson, 1976) whereas in the 'circular' burrowers, the mass is concentrated on the lower leg. These species tend to hop or scuttle rather than jump. The morphotype for a 'circular' burrower is a globose body with a small head, short legs and a well-developed inner metatarsal tubercle. A 'backwards sliding' burrower has longer legs, a more streamlined body and a well-developed inner metatarsal tubercle.

This study has shown a clear association between type of burrowing, musculature of the hind limb and morphotype.

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The Distribution of Four Species of Terrestrial Amphipods (Crustacea, Amphipoda: Talitridae) on Mt. Wellington, Tasmania

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ABSTRACT

Euterrestrial amphipods were collected from the south eastern slopes of Mt. Wellington, Tasmania. Four species were present: *Talitrus vulgaris*, *T. tasmaniae*, an undescribed species of *Talitrus* and an undescribed species of *Orchestia*. *Talitrus vulgaris* was found most commonly in gullies and at higher altitudes. *T. tasmaniae* was commonest at lower altitudes, while *T. sp.* became dominant at the highest sites (above 1000 m). The *Orchestia* species was confined to a small area at an altitude between 1000 and 1100 m.

On a transect across a small gully, *T. vulgaris* increased at the expense of the other two *Talitrus* spp. at the bottom of the gully. Pitfall trapping showed that *T. vulgaris* was active at a lower level in the litter than *T. tasmaniae*. Simple temperature and humidity tolerance trials showed that *T. tasmaniae* had a higher optimum temperature than the other *Talitrus* spp. and a slightly improved humidity tolerance at 95 and 97% RH.

Although *T. vulgaris* can partially exclude the other two *Talitrus* spp. in gullies, at many sites it coexists with them. Competition with *T. tasmaniae* is avoided by vertical separation in the litter. The basis of the coexistence with *Talitrus* sp. at high altitudes is unknown. *T. tasmaniae* appears to be an opportunistic species.

INTRODUCTION

Terrestrial amphipod crustaceans ("landhoppers") of the family Talitridae are common members of the litter fauna in the wetter forests of southern and eastern Australia, reaching very high abundances at some sites (1000 m⁻²) (Birch and Clark, 1953; Friend and Richardson, 1977). Recent unpublished studies (Friend, 1980) have shown that the Tasmanian fauna is diverse, having at least fifteen species in seven genera.

It is common to find more than one species of landhopper at sites in Tasmania (Friend and Richardson, 1977), and preliminary investigations by the authors on the slopes of Mt. Wellington revealed that three species were present there. These three species could be found in all combinations of co-occurrence and isolation, and no pattern in their distribution was immediately obvious. The aim of this

study is to describe the distribution of the landhoppers on Mt. Wellington, to elucidate as far as possible the factors limiting the distribution of each species, and to investigate the factors which permit the coexistence of species.

In order to achieve these aims, we have made an extensive survey of the distribution of landhoppers on the accessible south eastern slopes of Mt. Wellington and an intensive survey of their distribution across a forested gully. To investigate coexistence at a site, we have used pitfall trapping to examine the possibility of vertical zonation in the soil and litter (Friend and Richardson, 1977) and we have also examined the tolerances of the species to extremes of temperature and humidity.

The taxonomy of Australian terrestrial amphipods is currently in a state of flux, pending the formal publication of a revision prepared in a thesis by Friend (1980). Two of the species found on Mt. Wellington have been described: *Talitrus tasmaniae* Ruffo 1949 and *Talitrus vulgaris* Friend 1979. Hurley (1975) has proposed subdivisions of the unsatisfactorily large genus *Talitrus* into eight subgenera. Using Hurley's scheme the two named species and the remaining unnamed one can be more fully classified as *Talitrus* (*Mysticotalitrus*) *tasmaniae*, *Talitrus* (*Mysticotalitrus*) sp. and *Talitrus* (*Keratroides*) *vulgaris*. In the interests of brevity, the subgeneric names will not be used further here. During the course of the study, a further species, in the genus *Orchestia*, was collected. It is also included in Friend's (1980) revision, but must be referred to as *Orchestia* sp. here. Voucher specimens of all the species recognised in this study have been deposited in the Tasmanian Museum and Art Gallery, Hobart (Museum Numbers G2734-G2747 inclusive).

SITES

Mt. Wellington (1270 m) is the highest point of a block of high ground lying immediately to the west of the River Derwent. This block, produced by faulting, consists of sedimentary Permian and Triassic rocks overlain by a 350 m thick sill of Jurassic dolerite. Mountains of this form are common in south eastern Tasmania.

The soils of Mt. Wellington have been described by Martin (1940). Briefly, they consist of peaty High Moor and Skeletal soils on the summit plateau and upper slopes, and Podzols below 800 m. At higher altitudes, where erosion proceeds faster than weathering, boulder fields occur.

Although substantially colder than Hobart, the climate of Mt. Wellington is relatively mild. Average daily maximum and minimum temperatures at the summit range from 1.1 to 7.3°C, with an extreme range from about -6 to 30°C (Bureau of Meteorology, 1975), and although snow may fall in any month, severe frosts are uncommon (Richardson, unpublished data). Annual rainfall ranges from 700 mm on the lower slopes, to over 1400 mm at the summit, and the region above 600 m

is frequently covered with cloud. The south eastern slopes, where this study was carried out, are substantially shaded in winter.

The vegetation of the mountain has been described by Martin (1940) and Ratkowsky and Ratkowsky (1977), who proposed seven and twelve vegetation groups, respectively. For the purposes of this study, only five vegetation types were recognised. Arranged in ascending altitude, these were: (1) Gully Associations. These were dominated by *Bedfordia salicina*, *Pomaderris apetala*, *Olearia argophylla* and *Dicksonia antarctica*. *Atherosperma moschatum* was common in some gullies. Although small shrubs were absent, ground cover was provided by the ferns *Blechnum watsii* and *Polystichum proliferum*. Occasional *Acacia dealbata* were present in some gullies. The main components of the litter were leaves of *D. antarctica*, *B. salicina* and *O. argophylla*. *P. apetala* was less conspicuous in the litter as its leaves tend to decompose to a large extent before falling. The gullies had a rich, dark brown soil and a denser canopy than surrounding areas.

(2) *Eucalyptus obliqua* Associations. The main forest tree at lower altitudes was *E. obliqua* with an understorey of the three gully species (*O. argophylla*, *B. salicina* and *P. apetala*), combined with tall shrubs such as *Phebalium squameum*, *Zieria arborescens*, *Acacia verniciflua*, *Oxylobium ellipticum* and *Pultenaea juniperina*. These areas tended to have many fallen tree trunks, around which litter was built up off the ground to a depth of 30-60 cm. The litter was mostly eucalypt leaves and bark. The canopy was less dense than in the gullies and the soil was poorer and stonier.

(3) *Eucalyptus urnigera*, *E. johnstonii*, *E. delegatensis* Associations. At the upper limit of the *E. obliqua* association, a noticeable change in terrain occurred, with boulder fields becoming common, especially at higher altitudes. In these areas *E. urnigera*, *E. johnstonii* and *E. delegatensis*, and to a lesser extent *E. coccifera*, dominated. The understorey species were smaller and sparser than in the *E. obliqua* association with species such as *Hakea lissosperma*, *Pimelea nivea*, *Cyathodes dealbata*, *Pultenaea juniperina* and *Ghania psittacorum* dominating. The litter was predominantly eucalypt, built up thinly on top of the rocks. The canopy cover was further reduced and the soils were very stony.

(4) *Eucalyptus coccifera* Associations. At altitudes above 1000 m this was the dominant association. The ground cover was generally low (up to 30 cm), while in sheltered areas, shrubs up to 2 m developed, but *E. coccifera* was the only species of any height. Other species in this association included *Bauera rubioides*, *Coprosma nitida*, *Orites revoluta*, *Astelia alpina*, *Celmisia* sp. and *Poa* sp. There was no general build up of litter, but *E. coccifera* leaves tended to settle at the bases of the trees and between rocks. Canopy cover was less than in the other associations.

(5) Montane Shrubbery Associations. This association was confined to the highest altitudes (above 1200 m) on the summit plateau. Eucalypts were entirely

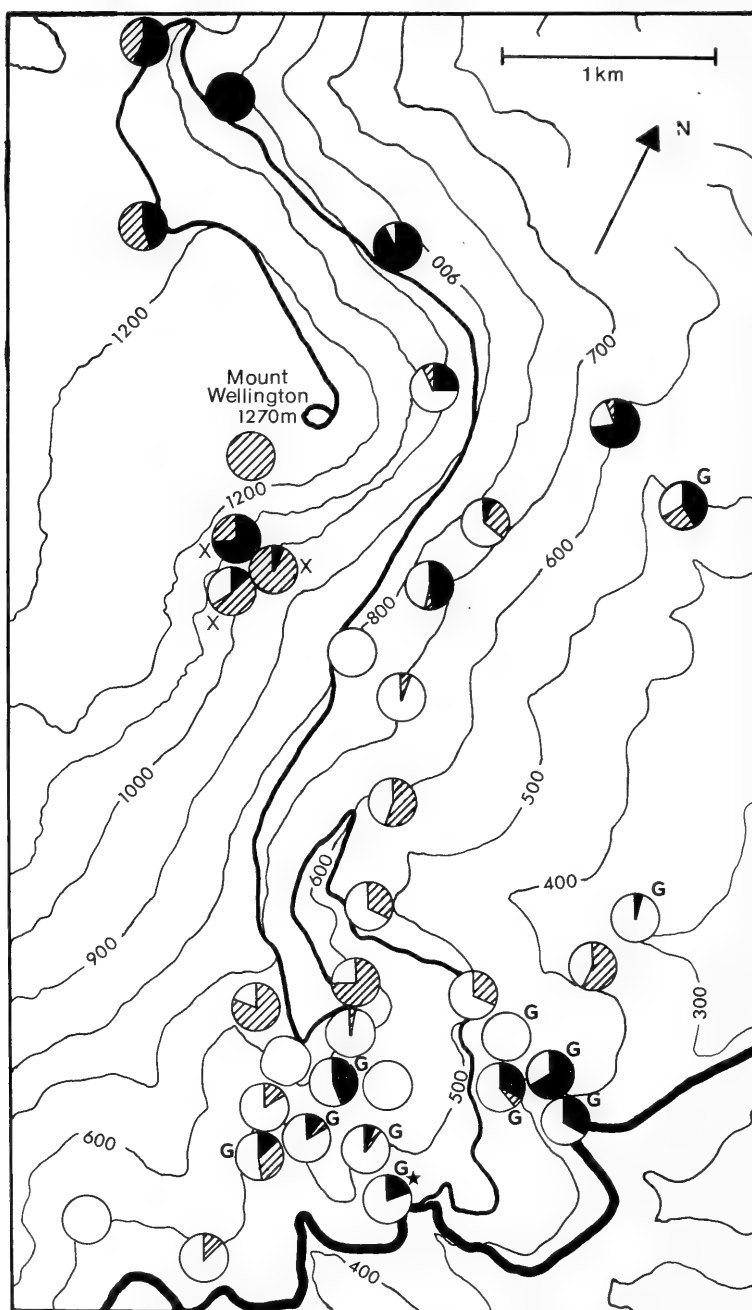


Fig. 1. The relative abundances of terrestrial amphipods found at 37 sites on Mt. Wellington. Sites classified as gullies are marked G. The Fern Glade intensive study site is marked with an asterisk. Solid: *Talitrus vulgaris*; cross-hatched: *Talitrus* sp.; open: *Talitrus tasmaniae*; cross: *Orchestia* sp. (presence only).

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absent and the tallest vegetation was a shrubbery (up to 1 m) consisting principally of *O. revoluta* and *Richea scoparia*. Much of the ground was bare rock or herbfield. There was only an occasional build up of litter where the tallest shrubs prevented the growth of ground layer plants.

All of these vegetation zones have been severely affected by fire at one time or another. The most recent fire to affect the whole area was in 1967, and much of the vegetation is regrowth from that time.

METHODS

EXTENSIVE SURVEY

Sites were sampled in two series, the first between August and October, 1980, the second in March 1981. In the first series, the litter from ten 625 cm² quadrats was collected from each site, while in the second, five quadrats of the same size were sampled at most sites. At the highest altitudes, the very rocky terrain and sparse vegetation resulted in such small amounts of litter that quadrat sampling was no longer appropriate, and such litter as could be found was collected by hand.

The litter was sorted by hand in a tray on the site and the amphipods were removed with an aspirator, preserved in 70% alcohol, and later identified in the laboratory.

The sites were classified into one of the five classes described above.

INTENSIVE SURVEY

A 140 m transect line was set up across the Fern Glade gully (Fig. 1), running approximately east-west. Amphipods were sampled at 10 m intervals along the transect, ten 625 cm² quadrats being taken at each station. The following parameters of the habitat were measured at each station: the moisture content of the soil and litter (weight loss after 50 h drying at 105°C); soil organic content (estimated as the weight lost after ignition at 450°C for 4 h); canopy cover, as estimated by the hemispherical photographic technique of Anderson (1964); litter depth (an average of three measurements at each site); and soil pH as measured by a CSIRO soil pH test kit.

PITFALL TRAPPING

Twenty-four pitfall traps were set up at each of three sites, one in the Fern Glade gully (F2) and two in the Jackson's Bend gully (J3 and J5). These sites, all of which were in gully vegetation associations, were chosen for their high densities of animals. Eight traps were placed at three different levels in the litter, that is, with the lip of the trap (1) level with the soil surface, (2) at the soil litter interface, and (3) approximately four centimetres below this interface. Quadrat samples for comparison with trap results were taken within the

vicinity of the traps to determine the proportion of amphipod species in the litter. Between August and October 1980, the traps were left for up to 36 days, or until a sufficient number of animals had accumulated.

The traps consisted of a plastic drinking cup of 7 cm diameter, protected from rain by a plastic Petri dish lid supported 50 mm above it on wooden legs. Those traps set below the litter surface were surrounded by plastic netting (mesh size 10 x 9 mm) which protruded above the soil surface and prevented debris from falling into the trap, while allowing unhindered access to the traps by the amphipods. Saturated aqueous picric acid was used as an odourless preservative.

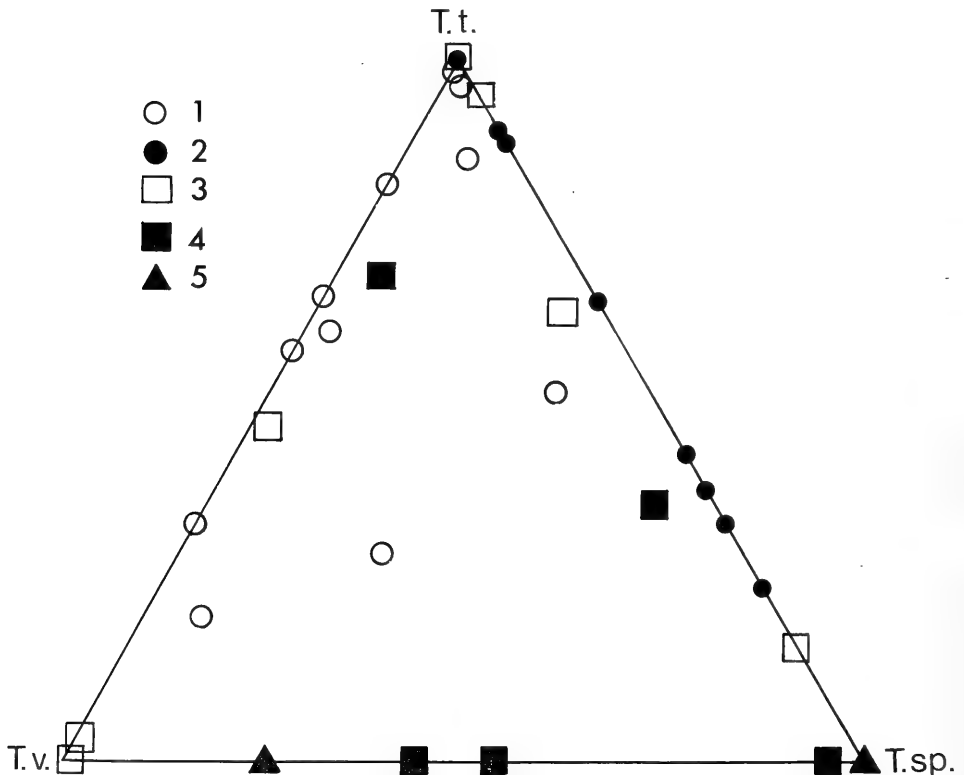


Fig. 2. Ternary Diagram showing the relative abundances of the three major species in the five habitat types recognised. The apices of the triangle represent 100% of each species. T.v.: *Talitrus vulgaris*; T. sp.: *Talitrus* sp.; T.t.: *Talitrus tasmaniae*. 1: Gully Associations; 2: *Eucalyptus obliqua* Associations; 3: *Eucalyptus urnigera*, *E. johnstonii*, *E. delegatensis* Associations; 4: *Eucalyptus coccifera* Associations; 5: Montane Shrubbery.

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TOLERANCE EXPERIMENTS

These were performed in chambers consisting of a plastic Petri dish with its base replaced by a fine nylon mesh, placed on the top of a similar dish containing a solution of KOH appropriate to the required humidity (Solomon, 1952). When the animals had been placed in the dish, a lid was taped onto the upper chamber. The animals were provided with food in the form of small pieces of leaves.

Temperature tolerances were tested at 100% relative humidity, using temperatures of 0°C, 5°C, 10°C, 15°C, 18°C, and 23°C. Groups of animals were acclimated at 5°C and 15°C before the experiment for 5 days. At least 20 animals of each species were used in each trial.

The humidity trials were carried out at 15°C, using 10 animals which had been acclimated at 15°C and 100% RH. Trials were carried out at 97%, 95%, 93%, 90%, 85% and 80% RH. The chambers were checked at regular intervals and the number of deaths noted.

RESULTS

During the study, five specimens of a fourth species of amphipod were collected from a very localised area immediately to the south of the Organ Pipes formation, at an altitude of between 1000 and 1100 m.

The proportions of species found at the sites examined during the extensive survey are shown in Figure 1. The number of animals collected at each site ranged from 8 to 366, but over 75% of samples contained more than 50 animals. While *Orchestia* sp. is very limited in its distribution, the other three species are found at almost all altitudes, but there is a substantial amount of variation in their proportions at the various sites. *Talitrus tasmaniae* is more prominent at the low altitude sites (i.e. below 800 m), while *Talitrus* sp. becomes dominant at the very highest sites. *Talitrus vulgaris* shows evidence of a discontinuous altitudinal distribution, being prominent both at low altitudes (below 500 m) and at high altitude (above 900 m).

Figure 2 shows the relative abundances of the three species plotted on a ternary diagram. The sites are distinguished on the basis of their vegetation. Few sites show anything approaching equal proportions of the three species, indeed only 10 out of the 37 sites contain all three species. One clear trend emerges from the vegetation records: The complete absence of *Talitrus vulgaris* from *Eucalyptus obliqua* associations. This is reflected in its under-representation from intermediate altitudes, where *E. obliqua* is the dominant tree. *T. tasmaniae* is absent from montane shrubbery, reflecting its absence from high altitudes; and from many gulley sites, but there are no other clear trends in the relationships between the proportions of amphipod species and vegetation type.

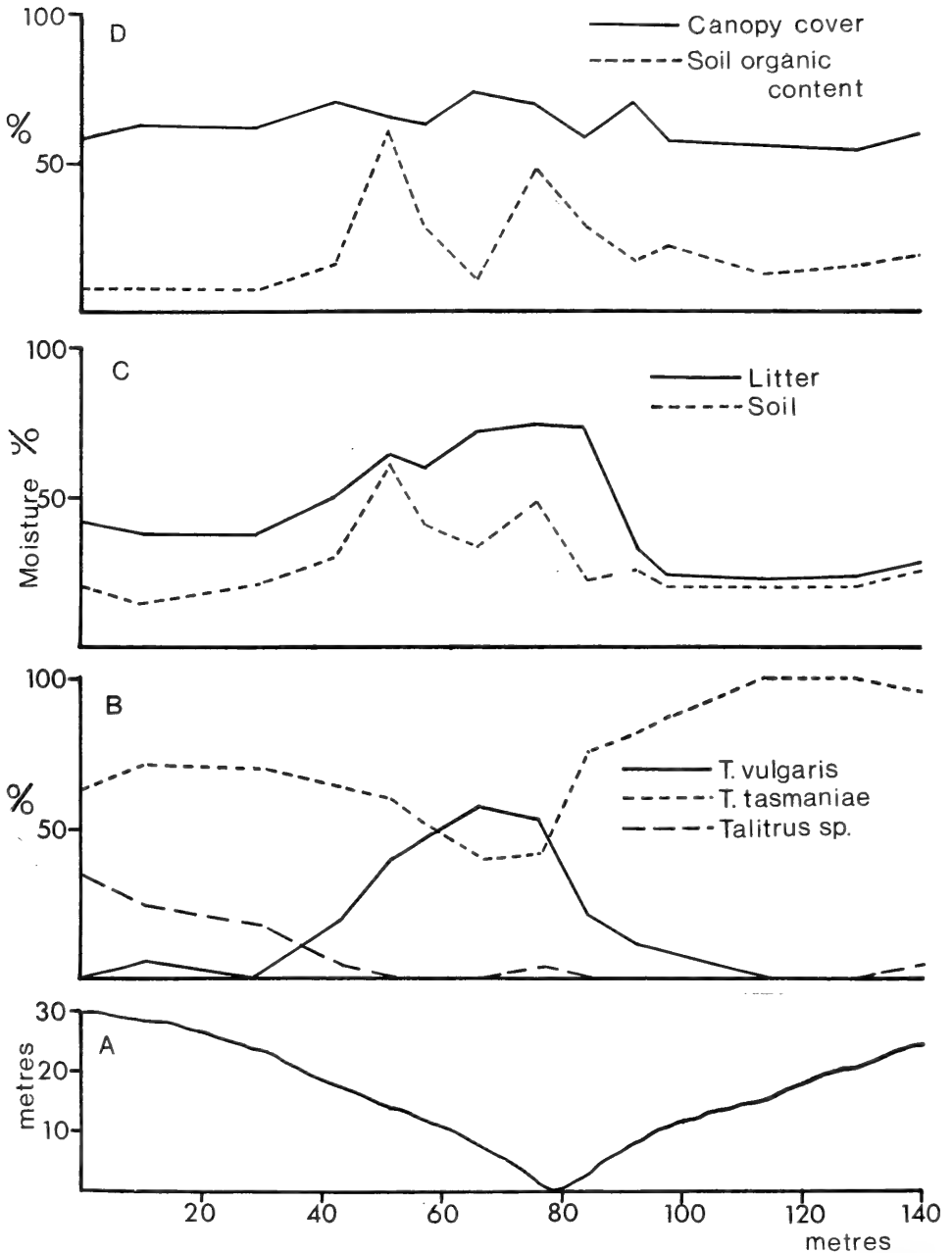


Fig. 3. Amphipod abundances and variation in physical parameters across the gully transect. A: profile of the gully; B: relative abundances (%) of the amphipod species; C: variation in litter and soil moisture; D: variation in canopy cover and soil organic content.

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Figure 3 shows the relative abundances of the three species on the gully transect, and the physical factors measured along it. *Talitrus vulgaris* clearly increases in the bottom of the gully, while *T. tasmaniae* and *Talitrus* sp. both decline. *T. tasmaniae* is much commoner on the western side of the gully.

Of the physical factors measured, soil and litter moisture content increase in the gully. Soil organic content reaches much higher values in the gully than on the slopes, although it varies considerably in the gully. There is a barely discernable decline in canopy cover at either end of the transect. Neither pH nor litter depth showed any systematic variation and have not been included on the figure.

TABLE 1. Frequencies of the three amphipod species captured in pitfall traps at three levels (Level 1: surface; Level 2: soil-litter interface; Level 3: 3-4 cm below soil-litter interface) at three sites: F2, J5, J3. The frequencies of the three species in quadrat samples taken at the same sites are also given. Figures in brackets are percentages. The chi-squared values compare the frequencies at each level with those from the quadrat samples. ***: $P < 0.005$; **: $0.01 > P > 0.005$; n.s.: not significant.

	<i>Talitrus tasmaniae</i>	<i>Talitrus</i> sp.	<i>Talitrus vulgaris</i>	Chi-squared
F2 Level 1	86 (95)	2 (2)	3 (3)	0.04 n.s.
Level 2	108 (94)	3 (3)	4 (3)	0.28 n.s.
Level 3	88 (92)	2 (2)	6 (6)	2.25 n.s.
Quadrat	134 (95)	4 (2.5)	3 (2.5)	
J5 Level 1	120 (92)	1 (1)	9 (7)	12.17 ***
Level 2	102 (83)	2 (2)	18 (15)	1.56 n.s.
Level 3	92 (77)	2 (1)	26 (22)	0.39 n.s.
Quadrat	252 (79)	6 (2)	61 (19)	
J3 Level 1	52 (95)	—	3 (5)	10.37 **
Level 2	82 (91)	—	8 (9)	11.27 ***
Level 3	70 (76)	—	22 (24)	0.0004 n.s.
Quadrat	131 (76)	—	55 (24)	

The results of the pitfall trapping are shown in Table 1. The catches from each of eight traps at the three depths have been amalgamated, and the proportions of species observed in the quadrat samples have been included for each site. The departure of the observed frequencies of species caught at each level from those in the quadrat samples were tested using chi-squared, and the results are included in the table. At site F2, none of the catches at any of the three depths differs from the overall proportion in the litter, but the numbers of *T. vulgaris* and *Talitrus* sp. are both low.

At site J5, the catch at the upper level contains more *T. tasmaniae* than expected, and fewer *T. vulgaris*, while the catch at the two lower levels does not differ from that in the quadrat sample.

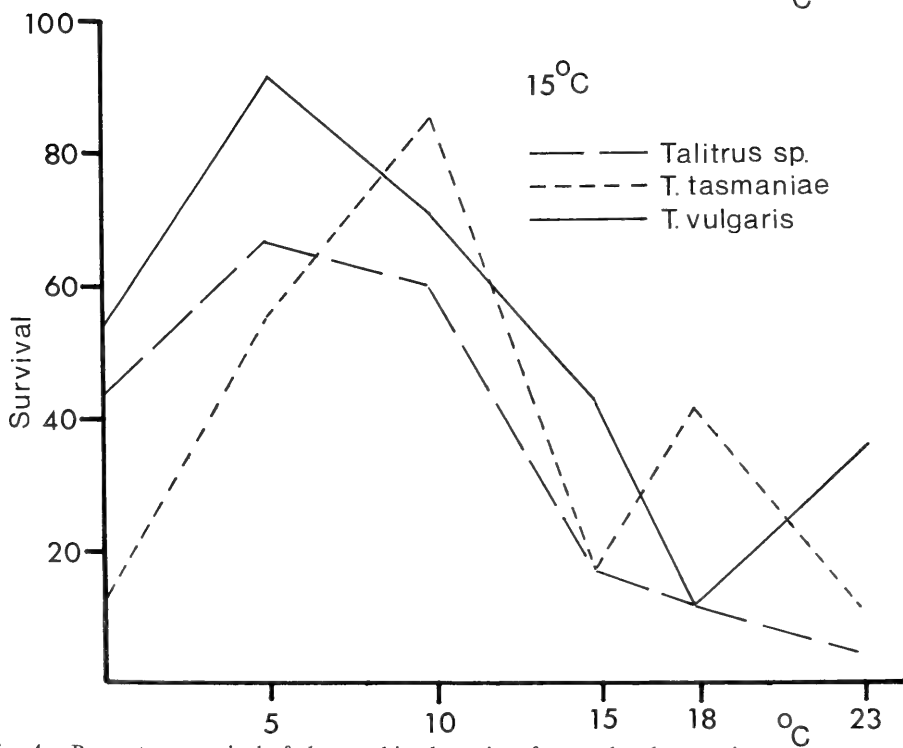
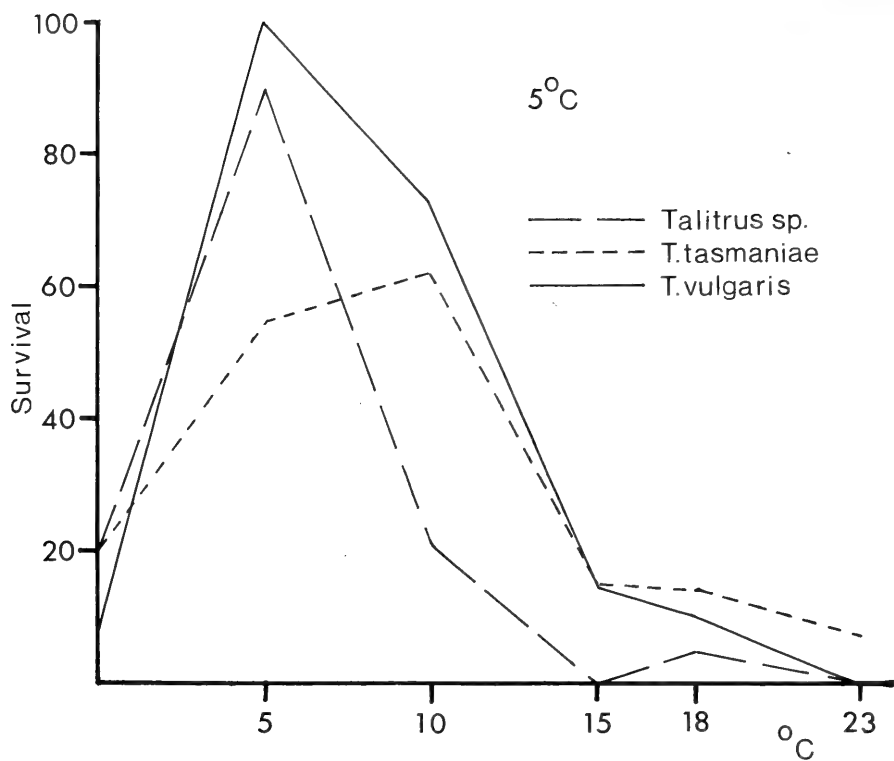


Fig. 4. Percentage survival of the amphipod species after twelve days at six test temperatures. The animals were acclimated to either 5° or 15°C.

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At site J3, the upper level catch also departs from the expected in the same way as at J5, and the same departure can be seen at the intermediate level, while the catch at the lower level resembles the quadrat sample once again.

It appears that *T. tasmaniae* is more active on the surface and in the upper layers than *T. vulgaris*, and this is apparently due to a vertical separation between the species, rather than differential activity, since the lowest level catch always reflects the overall litter proportions. If *T. vulgaris* were simply less active, and hence trapped less often, the lowest catch should reflect this as well as the upper ones.

In order to summarise the results of the temperature tolerance experiments, the percentage of survivors after 12 days exposure to the six test temperatures is plotted in Figure 4, for each acclimation temperature. At both acclimation

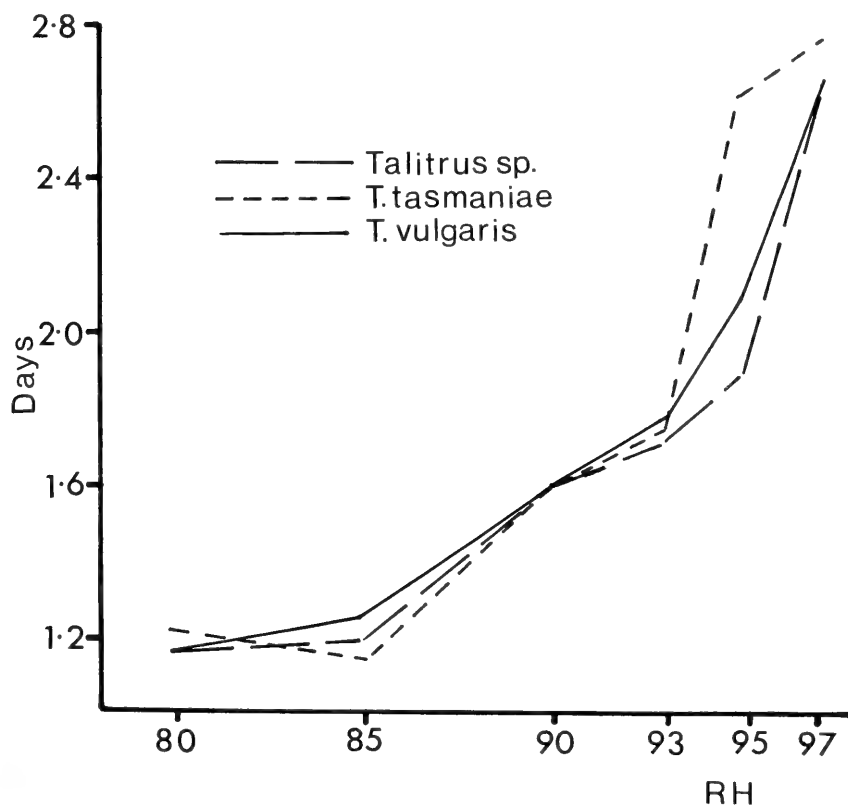


Fig. 5. Days required to produce 50% mortality of the three amphipod species at six test humidities. The tests were performed at 15°C.

temperatures, *T. vulgaris* and *Talitrus* sp. have their highest survival at 5°C. *T. tasmaniae* shows a higher optimum, 10°C, in both cases. The tolerance ranges of all three species are broadened after acclimation to 15°C and this is particularly marked in *Talitrus* sp.

Figure 5 shows the results of the humidity tolerance trials. Average survival declines sharply with decreasing humidity, and there is very little variation between the three species, apart from a suggestion of improved survival in *T. tasmaniae* at 95 and 97% relative humidity.

DISCUSSION

Although the distributional data collected here show no discrete differences between the three major species, there is circumstantial evidence to suggest how their distributions are controlled, and how they partition the available space when they coexist. Thus *Talitrus tasmaniae* is found most extensively at lower altitudes, where it is presumably able to colonise habitats not available to the other two species through its better tolerance of higher temperature (and there is also a suggestion that it has an improved tolerance to lower humidity), *Talitrus vulgaris* is most prominent in gullies and at high altitudes, which corresponds to its higher tolerance to cool conditions compared to *T. tasmaniae*.

Little can be seen in the data to separate *Talitrus* sp. from *T. vulgaris*. Its numbers decline sharply in the face of increasing numbers of *T. vulgaris* across the gully transect, and so, in the absence of any evidence from the tolerance experiments, it could be concluded that this is the result of competitive exclusion by *T. vulgaris*. However, at the higher altitudes, *Talitrus* sp. coexists with *T. vulgaris*, so in that situation, the latter's competitive ability has apparently been lost. It is worth noting that these observations have been made over relatively short periods of time, at a restricted time of year. It is possible that the proportions of species change from season to season as changes in the climate alter the balance of advantage from one species to another.

Talitrus tasmaniae is more active on the litter surface than are the other species, which is supported by the indication that it has better tolerance of high temperatures and lower humidities. It is possible that *T. tasmaniae* is an opportunistic, fugitive species (*sensu* Hutchinson, 1951), colonising new areas and eventually being outcompeted in them, except where its wider tolerances allow it to colonise areas unavailable to other species. Further evidence, in the form of long-term data on the changes in proportion of the species at a single site, and also on the distances moved by individuals of the various species, is needed to test this hypothesis.

Among the classical correlates of r-selected species are found small body size and high reproductive potential (Pianka, 1970). In terrestrial amphipods, these trends may be obscured because a) larger body size enables the female to

brood larger numbers of eggs, thus enhancing her reproductive potential, and b) larger size implies both a larger reservoir of water and a smaller surface area in relation to volume. Thus in these animals, large body size may be advantageous to a mobile species, within certain limits, and be associated with an increased reproductive potential. The upper limit to body size is likely to be set quite low by the animal's need to be able to find shelter in small spaces and crevices in the soil and litter.

Since no direct evidence of competitive exclusion can be presented here, some consideration must be given to the possible mechanisms which allow the species to coexist. Friend and Richardson (1977) investigated the coexistence between *Talitrus vulgaris* and a species not present on Mt. Wellington, *Talitrus* (*Keratroides*) *angulosus*. They suggested that there was a vertical separation between the two species, with *T. vulgaris* predominating in the upper and surface layers. *T. angulosus*, which is smaller, unpigmented and has reduced eyes and appendages, was found in the lower layers of the litter and in the soil. Friend and Richardson (1977) suggested that this separation was maintained by competition for space.

In that case, *T. vulgaris* was the upper litter species, whereas on Mt. Wellington, it is found in the lower layers, with *T. tasmaniae* above. However, while *T. angulosus* shows obvious adaptations to burrowing (pigmentation, length of appendages and body size), *T. vulgaris* and *T. tasmaniae* are superficially similar in those characteristics. It will be of interest to investigate the vertical separation in a site where all three species (*T. tasmaniae*, *T. vulgaris* and *T. angulosus*) occur together. Such sites have been recorded by Friend (1980), in Tasmania.

Examples of other soil macroarthropods which separate vertically in the soil and litter are given by Wallwork (1976). There is no evidence at present for any dietary separation in the niches of Tasmanian amphipods (Friend and Richardson, 1977; Friend, 1980).

Information on the geographical distribution of the three *Talitrus* species in Tasmania is given by Friend (1980). *Talitrus vulgaris* is the most widespread Tasmanian landhopper, occurring throughout the state. *T. tasmaniae* is the most restricted species of the three studied here, occurring only in the south east. *Talitrus* sp. has the same range as the latter, plus an extension into the west and south west. The very extensive distribution of *T. vulgaris* is paradoxical in view of its restricted distribution on Mt. Wellington. Friend (1980) makes no comment on the habitat preferences of this species, but notes that there are several forms within the species which may qualify for species rank. Differences in the tolerances of these forms may account for the restricted distribution observed here.

Because of its very restricted range, the discussion above has ignored the occurrence of the *Orchestia* sp. recorded for the first time on Mt. Wellington

in this study. This record extends the range of the species compared with Friend's (1980) records. The nearest previous records were from the Snowy Range at altitudes of 6-900 m, some 50 km south west of Mt. Wellington. This species of *Orchestia* might be expected on other outliers of the west and south west highlands, such as the Mt. Field massif and Wyld's Craig.

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Observations on the seasonal abundance and life history of some benthic invertebrates from Great Lake and Arthurs Lake, Tasmania

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ABSTRACT

Seasonal variation in abundance and brief details of the life history of species of chironomids, trichopterans, phreatoicids and oligochaetes from Great Lake and Arthurs Lake, Tasmania are presented. The data are compared with other studies of similar species elsewhere.

The seasonal abundance of the insect species as well as the phreatoicids could be related to the life history of each species. No consistent patterns were detected in the seasonal abundance of the oligochaetes studied.

INTRODUCTION

The only previous studies on the benthic invertebrate fauna of Tasmanian lakes are those of Weatherley and Nicholls (1955), and Timms (1978). These studies did not provide any data on seasonal variations in the fauna or on the life history of any species.

Data on seasonal variation and life history of benthic invertebrates in the lakes of mainland Australia are also sparse. Timms (1973) gives some details for several species in three Victorian lakes whilst Paterson and Walker (1974) studied the life history of a chironomid species in a Victorian saline lake.

One of the primary aims of a study of the benthic faunas of Great Lake and Arthurs Lake (Fulton, 1981) was to investigate seasonal variations in the faunas of those lakes. From the collections made it was possible to draw some conclusions as to the life history of the common species in various taxa. Other details of the faunas are reported elsewhere (Fulton, 1983 a, b).

MATERIALS AND METHODS

Series of samples were collected with an Ekman grab (232 cm²) from six sites in Great Lake (1975) and six sites in Arthurs Lake (1977-78). Twenty samples were taken at each site with the program commencing at the end of January in each case. Sampling was repeated at the end of every second month over a year in Great Lake and over 14 months in Arthurs Lake. The locations of the sample sites in each lake are given in Fig. 1. Various physical and chemical data relating to these sites are given in Fulton (1981).

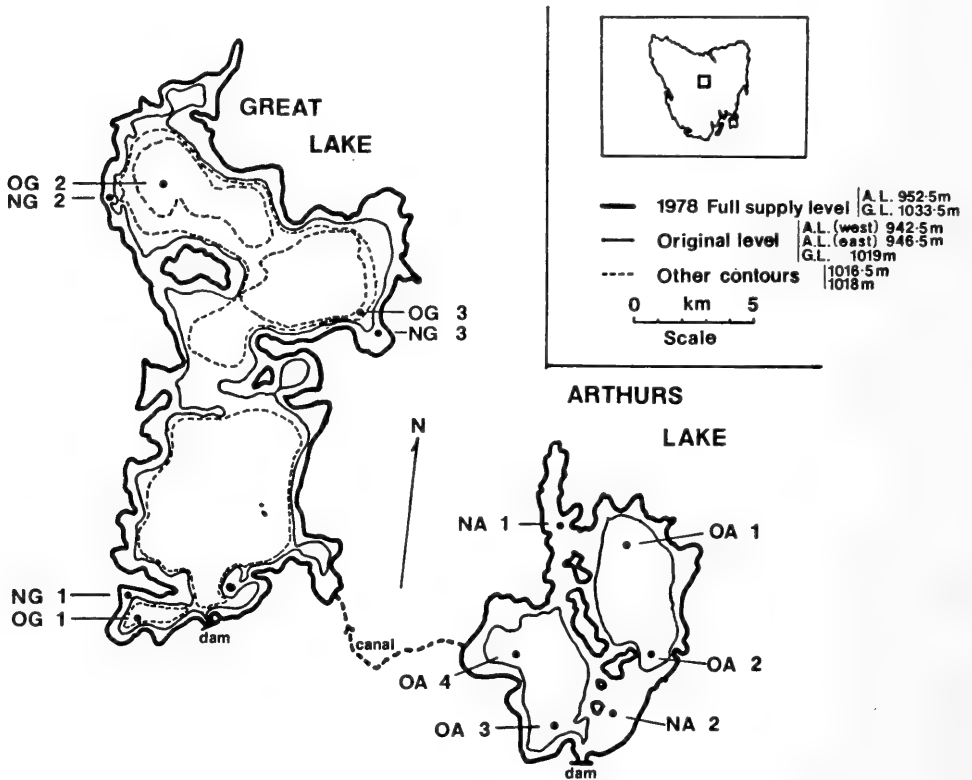


Fig. 1. Sample site locations within Great Lake and Arthurs Lake.

The animals were sorted from the substrate using an elutriation apparatus after that of Lauff *et al.* (1961). The material was passed through a 0.7 mm sieve. This sieve retained the vast majority of animals present in the sample with the exception of early instar stages of aquatic insects.

The basic data from which seasonal variation was observed were the total number of specimens present in each 20 sample series, converted to numbers per

OBSERVATIONS FROM GREAT LAKE and ARTHURS LAKE, TASMANIA

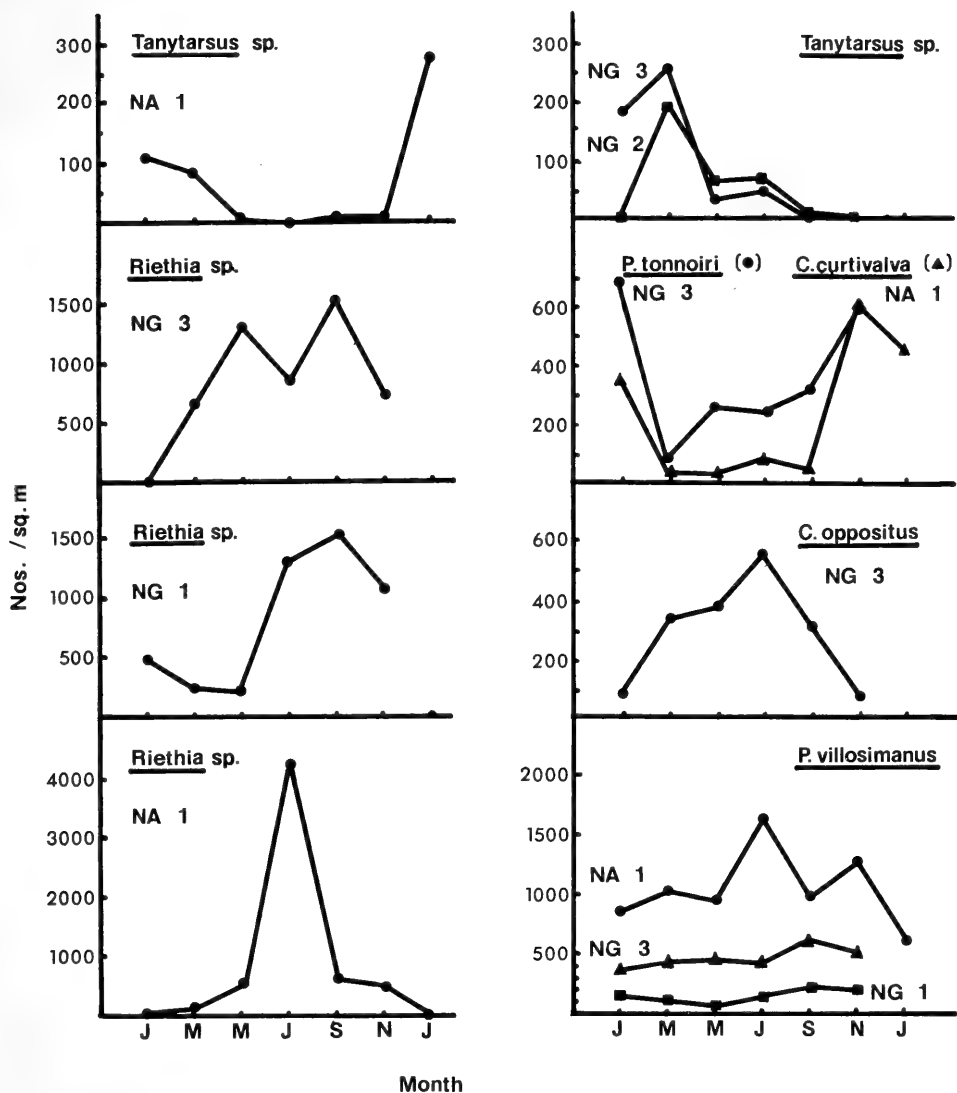


Fig. 2. Seasonal variation in abundance of various chironomid species from Great Lake and Arthurs Lake. Species and collection site are given on each graph.

square metre. Instar stages for chironomids and trichopterans were determined by head capsule width. Phreatic size frequency analysis was based on overall body length whilst the trichopteran measurements were of case length.

Specimens of *Riethia* sp., *Tanytarsus* sp. and *Colubotelson* sp., have been deposited in the Tasmanian Museum, Hobart, (registration numbers F1471, F1472, G2725 respectively) should comparisons be required.

RESULTS

The large sample series was designed to give a statistically reliable sample of the population in each case. Therefore, where some inference has been made from the observed variation in seasonal abundance of a species, the assumption has been made that such variation was not a result of errors in the sampling procedure.

SEASONAL VARIATION

Seasonal abundance data for each species in Great Lake and Arthurs Lake were collected but the variations could only be successfully analysed for the common ones. In most cases it was necessary for a species to be common at more than one site so that consistent trends could be detected. It can be seen from Figs. 2-6 that some species show obvious seasonal variations which are consistent between sites, whilst abundance peaks in other species appear unrelated for the various sites.

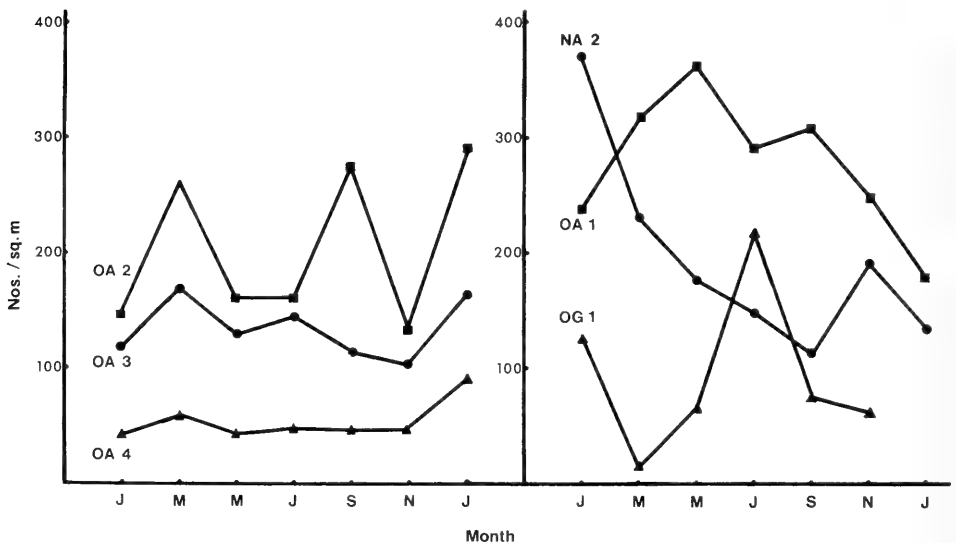


Fig. 3. Seasonal variation in abundance of *Coelopynia pruinosa* in Arthurs Lake and Great Lake.

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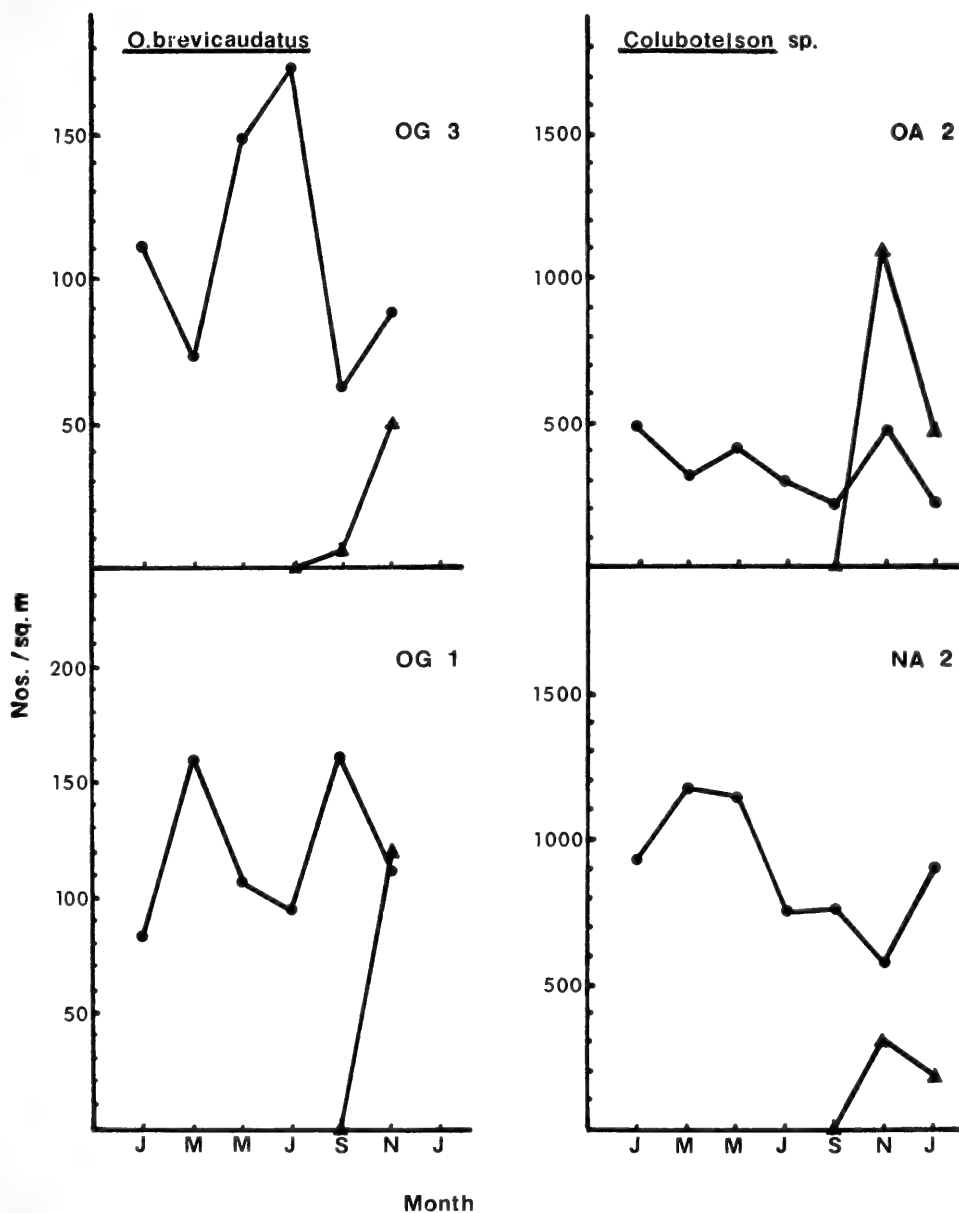


Fig. 4. Seasonal variation in abundance of two phreatoicid species at two sites in Great Lake and Arthurs Lake. New juveniles (▲) are shown separate from the rest of the population (●).

Chironomids: Many of the common chironomids in Great Lake and Arthurs Lake show marked seasonal variation in numbers. Distinct abundance peaks are evident in the species *Chironomus oppositus*, *Cladopelma curtivalva*, *Tanytarsus* sp., *Polypedium tonnoiri* and *Riethia* sp. (Fig. 2). From just five species there are four different peak abundance times with one species (*Riethia* sp.) showing variation between sites.

The peak in numbers of *Riethia* sp. occurs from July through September, whilst *C. oppositus* is most common in late July. *Tanytarsus* sp. was most frequent in March in Great Lake and January in Arthurs Lake. *C. curtivalva* and *P. tonnoiri* both show abundance peaks from November through January.

Another common chironomid species, *Procladius villosimanus*, does not exhibit consistent abundance peaks, (Fig. 2) although there was a peak in late July at one site. The occurrence data for *Coelopynia pruinosa* (Fig. 3) shows considerable variation between sites and seasonal variation patterns are difficult to interpret.

Phreotoicids: Considerable variations were observed in the number of adult *O. brevicaudatus* and *Colubotelson* sp. present at various sites in Great Lake and Arthurs Lake. Nevertheless, there is a consistent influx of juveniles occurring through October and November in both the Arthurs Lake and the Great Lake species (Fig. 4).

Oligochaetes: Of the common oligochaete species studied (*Haplotaxis ornamentus*, *Telmatodrilus bifidus*, and *Phreodrilus proboscidea*), none appear to show seasonal peaks that are consistent between sites (Fig. 5).

Trichopterans: Only one species, *Atriplectides dubius*, was common at any site (Fig. 6). Numbers of this species show a major peak in late September and a minimum in late May.

LIFE HISTORY

The seasonal variation in abundance of a species largely reflects the life cycle of that species. Some information on life history can be drawn from the seasonal variation data presented, whilst further analysis of the samples has added to this information.

Chironomids: Instar analysis data from chironomid samples were limited by the sorting technique. Numbers of the last two instars only of any species (in some cases only the last one) could be reliably estimated. The smaller early instars were able to pass through the sieve used to separate the animals from the substrate.

The percentages of larvae of various species in each instar stage are given in Tables 1 and 2. For *Riethia* sp., larvae in any stage other than final instar only occurred in January or March samples. From Table 1 and Fig. 2 it appears that

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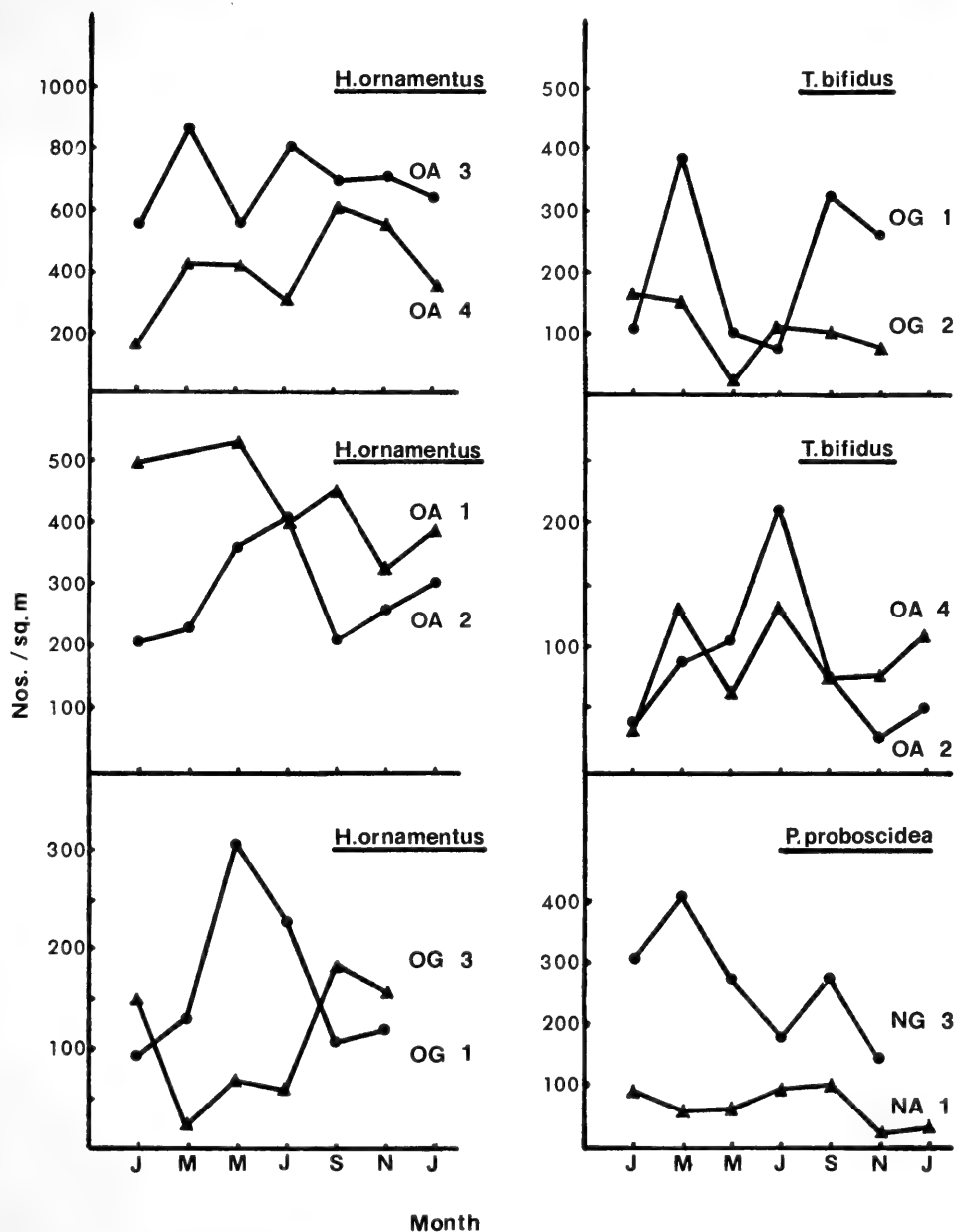


Fig. 5. Seasonal variation in abundance of three oligochaete species at various sites in Great Lake and Arthurs Lake.

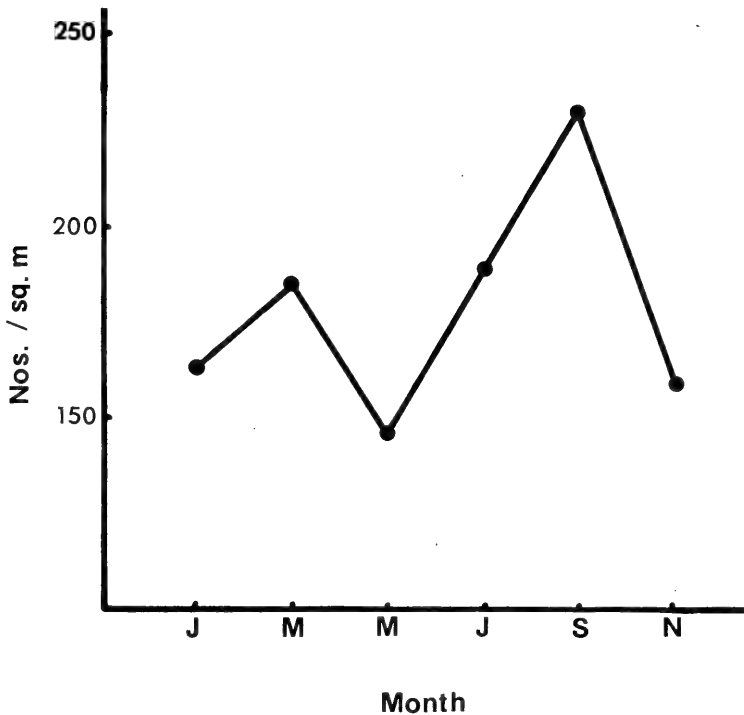


Fig. 6. Seasonal variation in abundance of *Atriplectides dubius* at site NG2.

Riethia sp. emerges in Great Lake and Arthurs Lake from spring to early summer. The new larvae grew to the fourth instar by March of the following year.

Both *Chironomus oppositus* and *Procladius villosimanus* have similar one year life cycles but there is some difference in the rate of growth through to the last instar. *C. oppositus*, from the instar analysis, emerged by mid-spring but the new generation took longer than *P. villosimanus* to reach final instar stage. *P. villosimanus* emerged about the same time as *Riethia* sp. but the young larvae apparently developed more rapidly. Although they only reached the final instar stage about the same time as *Riethia* sp. the third instar larvae were large enough after two months (the time of the following sample) to be retained by the sieve. This meant that no reduction in numbers of *P. villosimanus* was indicated in the abundance data (Fig. 2) even though instar analysis revealed that emergence had taken place (Table 1).

Polypedilum tonnoiri and *Tanytarsus* sp. also exhibit one year life cycles but emergence takes place later than the above three species. *P. tonnoiri* emerged in late summer and the new larvae developed slowly through winter to reach final

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TABLE 1. Percentage frequency of each instar of chironomids in samples from Great Lake and Arthurs Lake. (Total numbers are given in parentheses. Samples taken near end of month indicated).

Site	NA 1		NG 3		NA 1		NA 1		NG 3		NG 3		
Species	<i>Riethia</i> sp.		<i>Riethia</i> sp.		<i>P. villosimanus</i>		<i>C. oppositus</i>		<i>P. tonnoiri</i>		<i>Tanytarsus</i> sp.		
Instar	3	4	3	4	3	4	2	3	4	3	4	3	4
	%		%		%		%		%		%		
Jan.	33	67 (9)	—	100 (13)	87	13 (393)	3	94	3 (114)	1	99 (283)	3	97 (82)
Mar.	4	96 (55)	10	90 (413)	1	99 (467)	5	87	8 (122)	84	16 (31)	—	100 (115)
May	—	100 (265)	—	100 (580)	—	100 (440)	—	—	100 (160)	71	29 (103)	—	100 (18)
July	—	100 (1920)	—	100 (380)	2	98 (752)	—	7	93 (15)	69	31 (144)	—	100 (20)
Sept.	—	100 (295)	—	100 (690)	1	99 (448)	—	2	98 (251)	69	31 (141)	—	—
Nov.	—	100 (250)	—	100 (320)	7	93 (585)	—	—	100 (3)	6	94 (255)	—	—
Jan.	50	50 (2)	—	—	80	20 (276)	1	95	4 (602)	—	—	—	—

TABLE 2. Percentage frequency of each instar of *Coelopynia pruinosa* in samples from Great Lake and Arthurs Lake. (Total numbers are given in parentheses. Samples taken near end of month indicated).

Site Instar	NA 2			OA 1			OG 1	
	2	3 %	4	2	3 %	4	3	4
Jan.	—	30	70 (159)	—	41	59 (105)	14	86 (57)
Mar.	—	41	59 (102)	—	48	52 (145)	—	100 (7)
May	1	38	61 (77)	1	50	49 (150)	38	62 (24)
July	—	76	24 (66)	—	42	58 (134)	62	38 (89)
Sept.	—	73	27 (51)	—	53	47 (135)	42	58 (33)
Nov.	15	72	13 (89)	2	51	47 (109)	—	100 (20)
Jan.	—	57	43 (60)	—	6	94 (83)		

instar stage by late spring. *Tanytarsus* sp. emerged in autumn with final instar stage of the next generation being reached by mid-summer of the next year. As this species was quite small, it is likely that only the final instar was reliably sampled. The various instar stages of *Cladopelma curtivalva* were not examined but from the seasonal variation data for this species (Fig. 2) it is likely that it has a life cycle similar to that of *P. tonnoiri*.

The life cycle of the remaining common chironomid species, *Coelopynia pruinosa*, is more difficult to interpret. Data in Table 2 showed that there could be a significant proportion of larvae in each of the third and fourth instar stages at any time of year. The abundance data (Fig. 3) were generally inconsistent between sites although there were usually two peaks in each graph.

It is apparent that the life cycle is not of one years duration (c.f. Table 1) and from Table 2, two generations per year are suggested. A summer emergence is likely, whilst another emergence in May-June is indicated, particularly by the instar analysis of site NA2 and OG1 samples (Table 2).

Phreatoicids: Size frequency of samples of *Onchotelson brevicaudatus* from Great Lake (Fig. 7) and *Colubotelson* sp. (Fig. 8) from Arthurs Lake give some indication of the life history of these two species. The progression of the juvenile class is clearly seen with high mortalities occurring in this group before maturity.

The brood pouch was evident in female *O. brevicaudatus* in Great Lake in the three samples from the end of May until the end of September. Although some large specimens were still present after the influx of the young, it is unlikely that they survived to reproduce a second time. As the juveniles were still sexually undifferentiated after one year it is likely that they are in their second year before they reproduce.

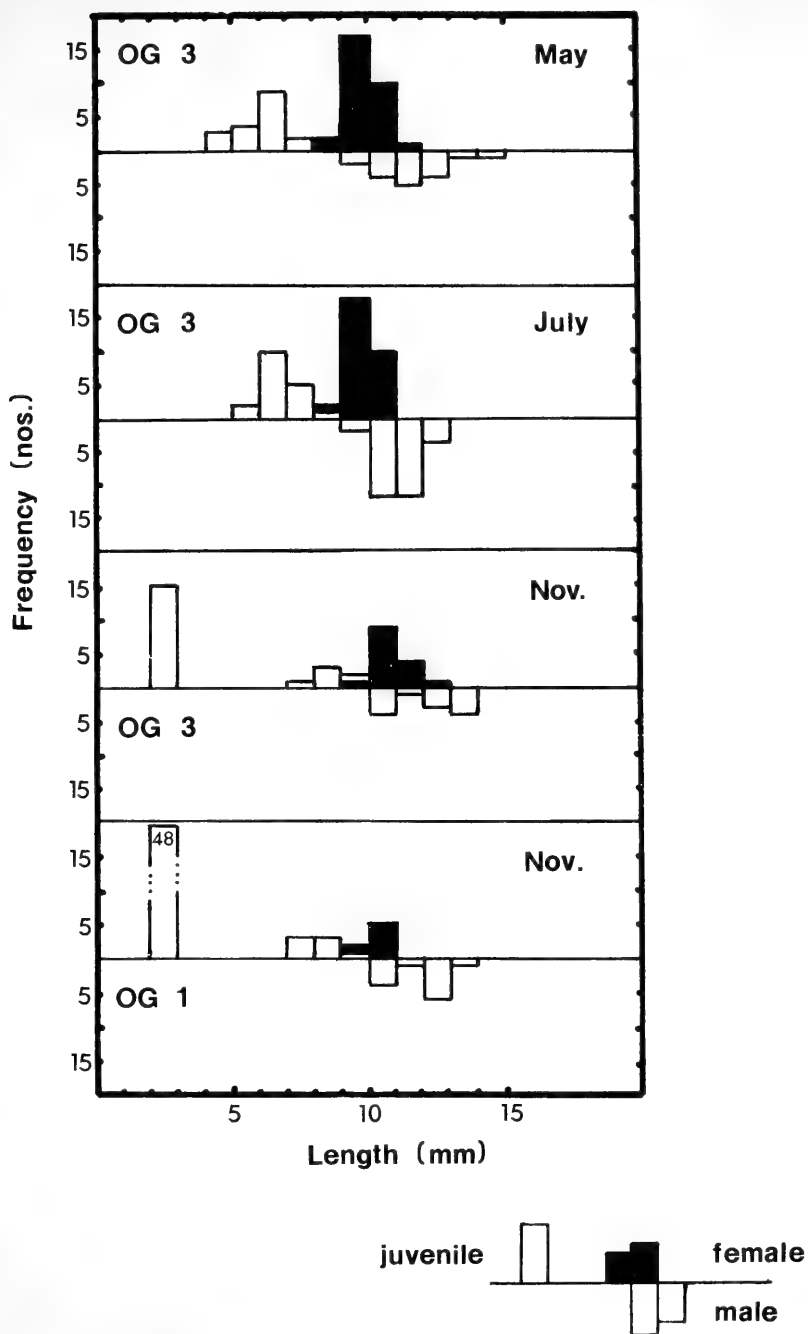


Fig. 7. Length (anterior margin of head to telson tip) frequency distribution of samples of *Onchotelson brevicaudatus* from Great Lake. Numbers within histogram indicate number in size class.

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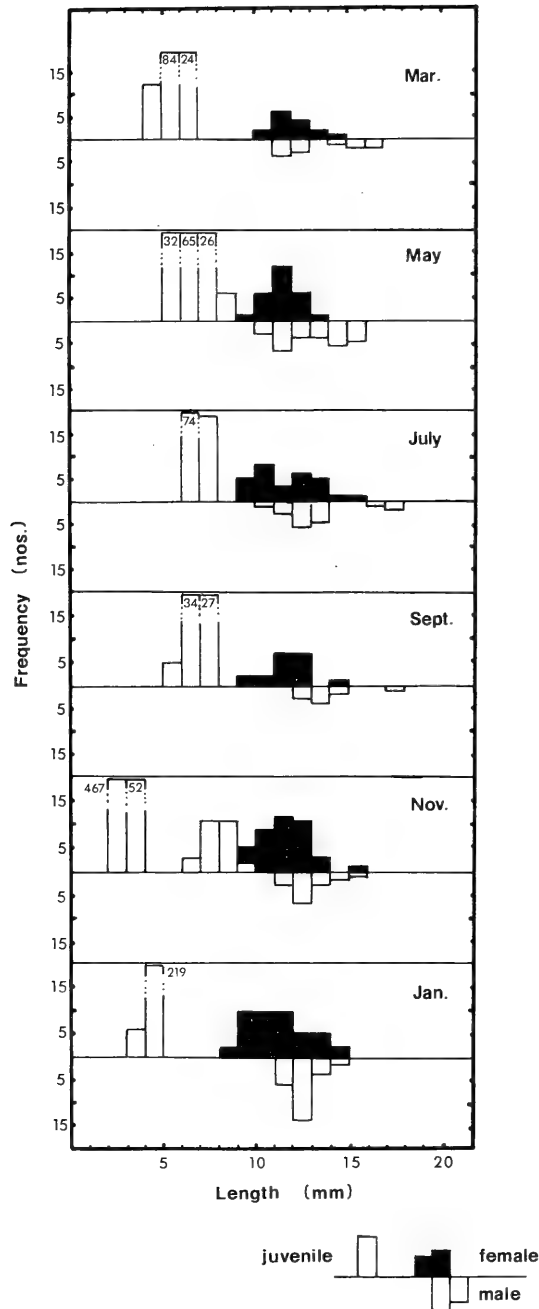


Fig. 8. Length-frequency distribution of samples of *Colubotelson* sp. from site OA2 in Arthurs Lake. Numbers within histogram indicate total number in size class.

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Colubotelson sp. follows a similar reproduction pattern to *O. brevicaudatus*. Copulating pairs of this species were observed in the late July samples in Arthurs Lake whilst females with brood pouches were most common in the late September samples. Juveniles first appeared in late November samples at all sites. Data in Fig. 8 suggest that *Colubotelson* sp. does not survive long after reproducing. The one year age group has become sexually differentiated between November and January but the mean size of both females and males has decreased. This suggests that the larger adults from November were no longer present.

There was also some evidence to suggest that there was an inverse relationship between the size of *Colubotelson* sp. and population density at the various sites. At site NA2, in Arthurs Lake, where the overall population density of this species was highest, specimens were consistently smaller than the corresponding stage at the other sites.

Oligochaetes: Although they were abundant the life cycles of the oligochaete species were not studied. There was no obvious juvenile influx into the populations and fragmentation of most specimens made the investigation of size classes very difficult.

Juvenile *Haplotaxis ornamentus* were collected in small numbers during the latter half of the year but these numbers had no significant effect on the seasonal abundance (Fig. 5). Cocoons containing single eggs of this species were collected with the mid-year samples from both lakes.

Trichopterans: The life cycle of *Atriplectides dubius* was examined at one site only, (NG1). The length-frequency distributions of the cases of this species are given in Fig. 9 whilst the percentage of the samples in each instar are given in Table 3. The instar analysis, based on head capsule width, revealed four separate instars. It was assumed that there was one smaller instar which was not recorded as it was small enough to pass through the sieve used.

TABLE 3. Percentage frequency of each instar of *Atriplectides dubius* in samples from site NG 2. (Samples taken near end of month indicated).

	Instar				Total nos.
	2	3	4	5	
	%				
Jan.	30	37	23	10	43
Mar.	—	22	23	55	88
May	—	41	21	38	61
July	—	46	23	31	92
Sept.	2	19	40	39	93
Nov.	—	15	15	70	73

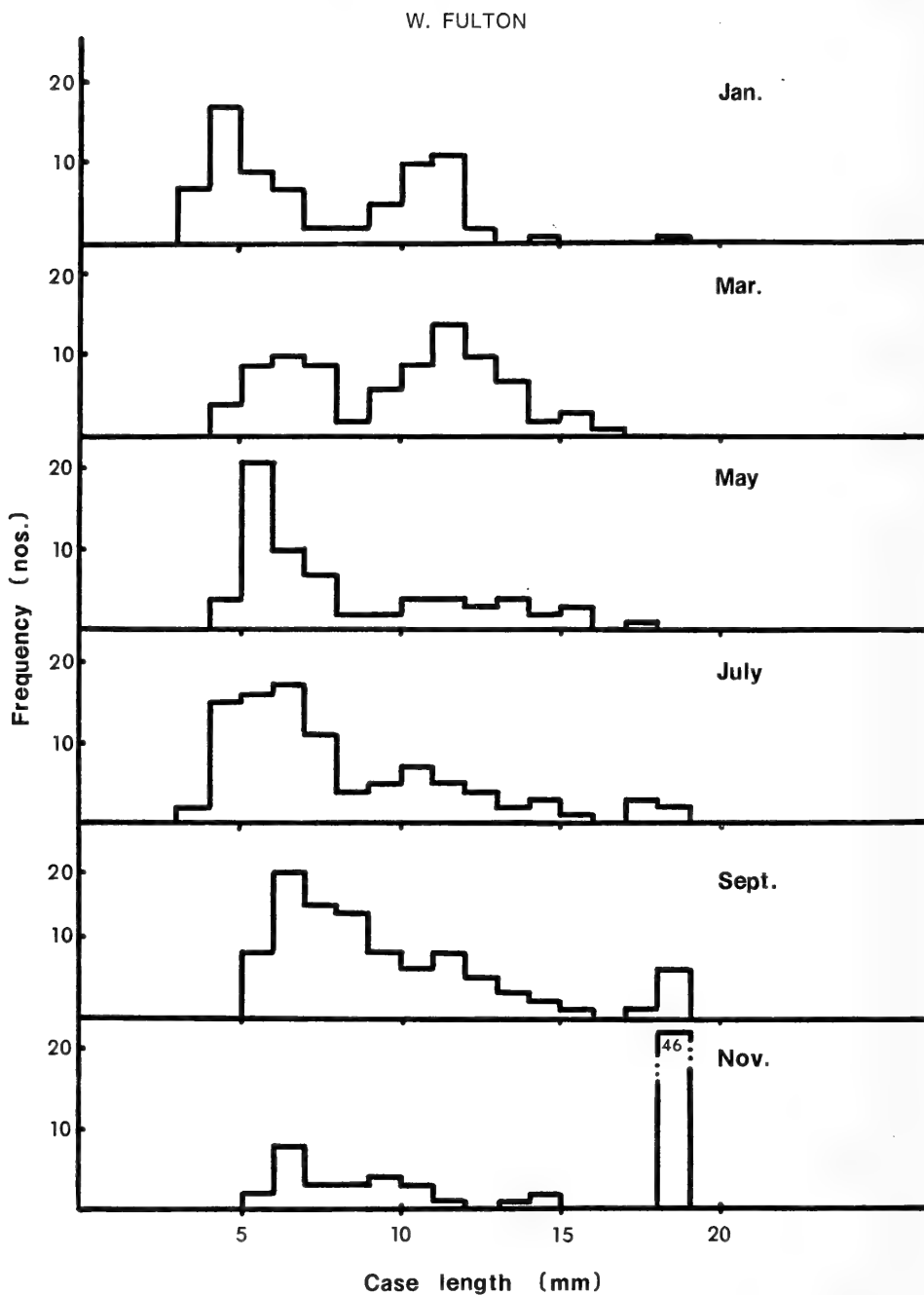


Fig. 9. Case-length/frequency distribution of samples of *Atriplectides dubius* at site NG2 in Great Lake. Numbers within histogram indicate total number in size class.

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The pupae of *A. dubius* were about 18 mm total length. When pupating, the larvae detaches about 7-8 mm of the posterior part of its case and places this across the entrance to seal it. Therefore larvae above 18 mm in case length were all grouped together in Fig. 9. Pupating larvae were found predominantly in late November samples.

There are two possible explanations for the two peaks observed in the histograms (Fig. 9). It could indicate a two year life cycle and therefore two year classes are present. It is more likely that there are two generations per year with a major emergence in November-December and a further emergence between April and late May.

The analysis of instars (Table 3) suggests a December hatching with a juvenile influx in January. The high proportion of final instar larvae in March parallels the length data in Fig. 9, but the decrease in proportion of this group in the following sample as well as a decrease in abundance overall (Fig. 6) indicates that another emergence has taken place in autumn.

DISCUSSION

The results have shown that the seasonal variations in abundance of the various species studied can often be explained by examination of the life history of each species. The chironomids all have emergence periods somewhere in the spring-summer period and this emergence time is usually reflected in the abundance data. Some of the data suggest that emergence times and abundance peaks are a little earlier in Arthurs Lake than Great Lake.

Procladius villosimanus was briefly studied by Timms (1973) in Victoria. He found that there was probably only one generation per year with emergence taking place in summer and early autumn. The Arthurs Lake data for this species suggests a similar one year life cycle but a slightly earlier emergence time in Tasmania. Timms (1973) also studied *Coelopynia pruinosa* in Victoria. He cautiously suggested that this species had a one year life cycle with emergence mainly in summer. The inconsistency of abundance and instar data for this species at different sample sites in Great Lake and Arthurs Lake also suggests that conclusions should be made with caution although it appears likely that *C. pruinosa* has two generations per year in Great Lake and Arthurs Lake. Emergence trapping would be required to confirm this.

The other species studied all appear to have one generation per year with distinct emergence times. None of these species have been studied elsewhere. Data on life history of some congeneric species are given by Timms (1973) and Paterson and Walker (1974).

With the exception of the juvenile influx there is no consistent pattern in the seasonal abundance of the phreaticids. In both *Onchotelson brevicaudatus* and *Colubotelson* sp. the seasonal patterns have different adult peak abundances which

do not appear related to their life history. It is likely that these species show contagious distribution patterns (Fulton, 1981) and the observed abundance fluctuations therefore may not reflect the true situation.

The life history of *Colubotelson* sp. has been studied before (Engemann, 1963; Knott, 1971). Knott suggested a two year life cycle for this species in south-eastern Tasmania and this is supported by the Arthurs Lake data. The Great Lake species, *O. brevicaudatus*, has not previously been studied. It appears to have a similar life cycle to *Colubotelson* sp.

Observed peaks in abundance of oligochaetes at the various sites appeared unrelated to each other. Few studies have recorded consistent seasonal variations in this group. A four year study of the tubificid *Potamothenis hammoniensis* in Lake Esrom, Denmark (Jonasson and Thorauge, 1972) failed to find repeated abundance peaks. Whilst the study of Great Lake and Arthurs Lake was not as extensive, it is nevertheless difficult to explain the inconsistencies between sites in the same lake, particularly when the spatial distribution within a site of *H. ornamentus* for example, was found to be regular at some sites (Fulton, 1981).

Interpretation of the life cycle of *Atriplectides dubius* is tentative in the absence of comparative data for other lacustrine benthic trichopterans in Australia. However, there is good agreement between the abundance, length frequency and instar data which suggest that this species has two generations per year. This should be checked by light trapping.

The data presented on life history and seasonal variation in abundance of several species of benthic invertebrates from Great Lake and Arthurs Lake show little variation between the two lakes even though collections were made in different years. None of the suggested life cycles appear unusual for the groups concerned although little comparative data are available.

ACKNOWLEDGEMENTS

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Rosellas, *Platycercus* spp., and their hybrids in the eastern Queensland-New South Wales border region.

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ABSTRACT

The results of a survey conducted within the Gold Coast hinterland and far northern N.S.W. region showed that while Eastern Rosellas (*Platycercus eximius*) and Pale-headed Rosellas (*P. adscitus*) were common, Crimson Rosellas (*P. elegans*) were relatively uncommon and largely restricted to more heavily vegetated habitats. The distribution of Eastern and Pale-headed Rosellas in timbered farmlands showed overlap; Pale-headed Rosellas were somewhat more common in urban areas than Eastern Rosellas. Mixed flocks of the two species were rare, but nearly 4% of sightings included hybrids between these species. The significance of hybridization between the species is discussed.

INTRODUCTION

In southeastern Queensland and northeastern N.S.W. the distributions of three rosella species overlap. They are the Crimson Rosella (*Platycercus elegans*), the Eastern Rosella (*P. eximius*) and the Pale-headed Rosella (*P. adscitus*). The Crimson Rosella which ranges from the Atherton Tableland in northern Queensland to southeastern South Australia is typically found in humid and semi-humid coastal forests including rainforests and sclerophyll forests; and may replace the Eastern Rosella at higher altitudes and in more heavily forested areas. The Eastern Rosella is found normally in savanna woodland and farming areas in southeastern Australia from southeastern Queensland to southeastern South Australia and Tasmania; the Pale-headed Rosella occurs in northeastern Australia from Cape York Peninsula to northern N.S.W. in lowland savanna woodland and sparsely timbered farmlands (Forshaw, 1969).

Hybrids between Crimson and Eastern Rosellas appear to be rare (Rogan, 1966; Courtney, 1967) while hybridization between the Eastern and Pale-headed Rosellas, although uncommon, has been reported (Brereton & Sourry, 1959; Keast,

1961; Forshaw, 1969). Indeed Keast (1961) suggested that the ecological relationship between these latter two morphologically distinct but closely related species was unclear. Certainly the habitat requirements of the two species appear to be similar although there is evidence of significant differences in their feeding biology (Cannon, 1981).

This paper presents the results of a survey conducted within the Gold Coast hinterland and far north eastern N.S.W. region which is an area where the ranges of all three rosella species overlap. Particular attention was paid to areas where both Eastern and Pale-headed Rosellas occurred and to their hybridization.

MATERIALS AND METHODS

Seven bi-monthly surveys were conducted from March 1978 to April 1979 from Surfers Paradise in Queensland in the north to Kingscliffe in N.S.W. in the south, and up to approximately 23 km inland from the coast. Approximately 400 km were traversed by car during each survey involving 200 survey points at about 2 km intervals (the same sampling sites were used on successive surveys — within 50 m). Sufficient time was spent at each stop to detect whether rosellas were present, usually about 10 minutes; the number and species of birds (where possible) and a brief habitat description was recorded. Where two or more species were seen within 1 km of each other, particular attention was paid to plumage to check for hybridization. Confusion can arise in differentiating between juvenile Pale-headed Rosellas and hybrids between Pale-headed Rosellas and Eastern Rosellas, particularly with regard to the extent of red suffusion on the crown. Hybrids were recognised as either birds having a general Eastern Rosella appearance but lacking the red on the head or breast, or birds resembling a Pale-headed Rosella but possessing red markings on the head far more extensive than typically found in juvenile birds and/or the presence of red on the upper breast. Birds were accepted as hybrids if they lacked the usual plumage characters of either the Pale-headed or Eastern Rosella, or had a mosaic of plumage features.

Using both aerial photographs (Murwillumbah series I-IV, 9541, 1975; Queensland Department of Mapping and Surveying) and the vegetation map of McDonald & Whitman (1979) a simplified habitat map of the survey area was prepared. Three broad habitats were recognised (a) urban development, (b) agricultural land and (c) forest areas. The first two habitats comprise disturbed areas where vegetation had been cleared or substantially modified. These habitats ranged from totally cleared areas (such as canal development) to areas with scattered vegetation, essentially open woodland communities. The last category, forest areas, are mainly open-forest comprising *Eucalyptus* communities, but with very limited amounts of tall-closed forest, and littoral or mangrove vegetation (see McDonald & Whitman, 1979 for greater details).

ROSELLAS AND THEIR HYBRIDS

RESULTS

During the survey a total of 1517 stops were made, 420 (27.7%) in urban areas, 944 (62.2%) in open agricultural areas and 153 (10.1%) in forested areas (see Table 1). Thus nearly 90% of the surveyed area consisted of habitats altered by man in varying amounts. Crimson Rosellas were relatively uncommon, being recorded in only 26 of the 1517 stops; 69.3% of these observations were recorded in forest areas. Crimson Rosellas were located mainly at the heads of the Bonogin, Tallebudgera and Currumbin Creek systems in Queensland, near Mt. Tomewin and to restricted areas of forest in northern N.S.W. No Crimson Rosellas were seen in urban areas and only 31% of sightings of this species were in open agricultural areas.

TABLE 1. The distribution of spot sightings of rosellas (including single species flocks, mixed species flocks and mixed or single species flocks with hybrids) in three habitats in southeastern Queensland and northeastern N.S.W. between March 1978 and April 1979.

	Habitat type			Total N
	Urban	Agricultural	Forest	
Total No. of stops in each habitat	420	944	153	1517
% of total stops in each habitat	27.7	62.2	10.1	
No. of stops where Eastern Rosellas recorded	1	71	9	81
% of total Eastern Rosella sightings	1.2	87.7	11.1	
No. of stops where Pale-headed Rosellas recorded	15	92	15	122
% of total Pale-headed Rosella sightings	12.3	75.4	12.3	
No. of stops where Crimson Rosellas recorded	0	8	18	26
% of Crimson Rosella sightings	0.0	30.8	69.2	

Eastern and Pale-headed Rosellas were sighted more frequently, particularly in open agricultural areas, rarely in urban areas, although 12.3% of Pale-headed Rosella sightings were in urban areas around Currumbin and Burleigh in Queensland and Tweed Heads West in N.S.W. Both species were typically seen inland from the immediate coastal area, the Pale-headed Rosella being more common in the northern part of the survey area and the Eastern Rosella in the extreme south. The Pale-headed Rosella was the most common of the three species (Table 2) and each species was generally sighted separately, usually alone or as a pair. The means and ranges of bird numbers of single species sightings are as follows:

Crimson Rosella 1.8 ± 1.7 (range 1-9, $N = 24$), Eastern Rosella 1.9 ± 0.9 (range 1-6, $N = 59$) and Pale-headed Rosella 1.7 ± 0.8 (range 1-7, $N = 100$).

Eastern and Pale-headed Rosellas were seen in the same general area (defined as within 200 m) at the same time more frequently than the other species combinations. However a mixed flock of these two species without hybrids was only seen once. More commonly there were areas where two or more species were seen but at different times. Given that rosellas are reasonably sedentary (Brereton, 1971 a, b) the occurrence of rosellas within the same area was defined as observations recorded within 1 km². To assess how frequently Eastern and Pale-headed Rosellas were recorded within the same area a grid system of 1 km squares was superimposed on a distribution map of the two species employing the Transverse Mercator Projection (Zone 56, Australian National Spheroid). Figure 1 shows schematically the presence (but not the number of observations) of Eastern and Pale-headed Rosellas within this grid system. Pale-headed Rosellas were recorded alone in 36 of the 93 squares (38.7%) within which birds were recorded in the grid system, the Eastern Rosella alone in 22 squares (23.7%) and both species together in 27 (29.0%) of squares. Mixed species groups with hybrids occurred in only 5 of the squares (5.4%), Eastern Rosellas with hybrids in 1 square (1.1%), Pale-headed Rosellas with hybrids in 1 square (1.1%) and hybrids alone in 1 square (1.1%).

TABLE 2. Sightings of rosella species in southeastern Queensland and northeastern N.S.W. from March 1978 to April 1979 summarised from each spot sighting survey during the seven bi-monthly surveys.

	Species	No. of sightings	%	No. of sightings	%
Single species sightings	Eastern	59	28.2	183	87.6
	Pale-headed	100	47.8		
	Crimson	24	11.4		
Two species seen at same time within 200 m but not in the same flock*	Eastern + Pale-headed	15	7.2	17	8.1
	Eastern + Crimson	1	0.5		
	Pale-headed + Crimson	1	0.5		
Two species seen within the same flock	Eastern + Pale-headed	1	0.5	1	0.5
Hybrid sightings	Eastern + Pale-headed + hybrid	4	1.9	8	3.8
	Eastern + hybrid	1	0.5		
	Pale-headed + hybrid	1	0.5		
	Hybrid alone	2	1.0		
Total		209		209	

* Grouping of birds in this group as one observation accounts for the difference in total number of records given in this Table when compared with Table 1.

ROSELLAS AND THEIR HYBRIDS

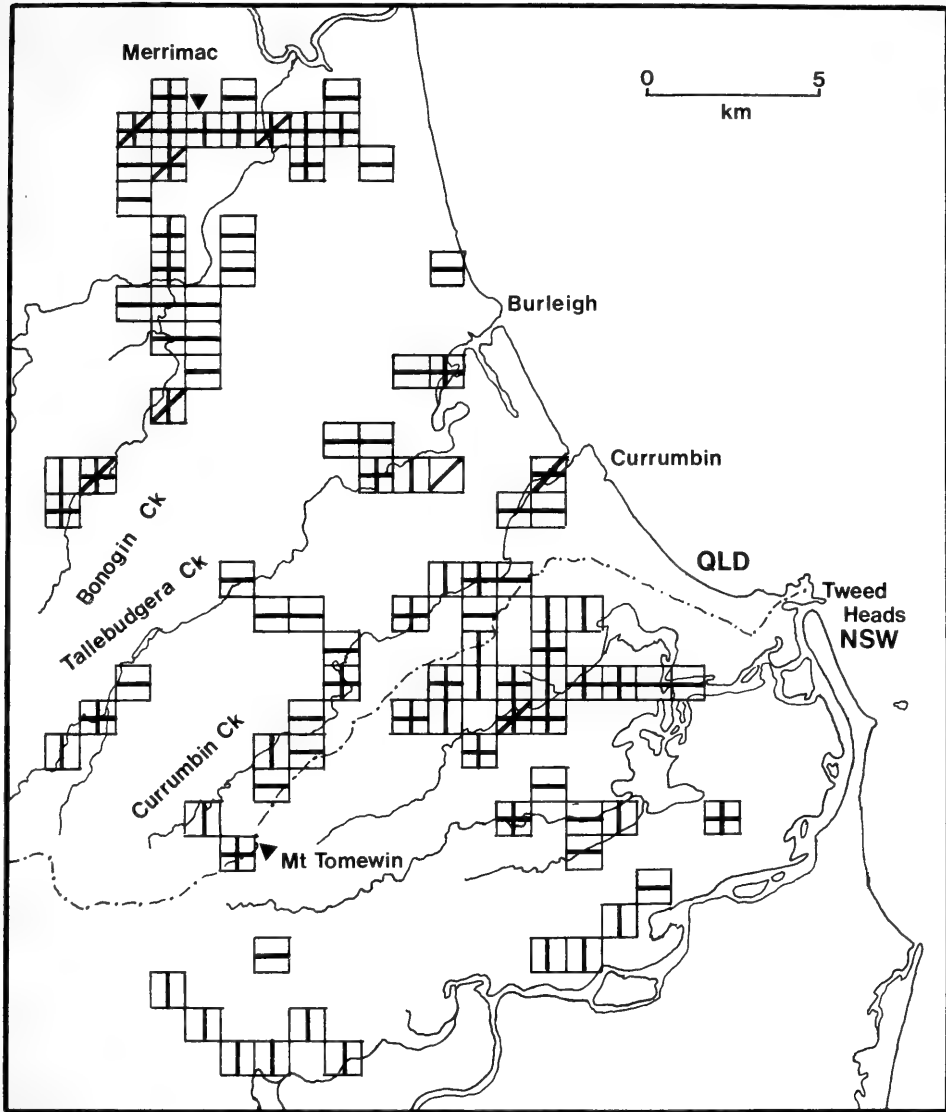


Fig. 1. Presence of Eastern Rosellas (vertical lines), Pale-headed Rosellas (horizontal lines) and their hybrids (diagonal lines) within one square kilometre grids in the Queensland-N.S.W. border region (border shown as dotted line). Crimson Rosellas not shown since no hybrids between this species and either of the other two species were seen.

TABLE 3. Sightings of Eastern Rosellas (ER), Pale-headed Rosellas (PHR) and Eastern x Pale-headed Rosella hybrids (ER/PHR) in southeastern and northeastern N.S.W. showing hybrid species associations.

Type of assoc.	Date of sighting	Total No. birds	No. hybrids	No. ER	No. PHR	Area	Activity of group	Appearance of hybrid
Mixed species	13.4.78	8	2	4	2	1.5 km WSW Merrimac Qld.	feed	like PHR with extensive red on head and breast
	13.4.78	35	+	+	+	1.8 km WSW Merrimac Qld.	feed	no detailed description several ER/PHR intermediates
	31.5.78	7	1	4	2	2 km E Merrimac Qld.	perch	like PHR with extensive red on head
With Eastern	20.7.78	5	1	3	1	Bonogin Rd. 6.5 km SSE Mudgeeraba Qld.	perch	hybrid perched close to PHR, like PHR faint red upper breast
	20.7.78	2	1	1	—	Bonogin Rd. 4 km S Mudgeeraba Qld.	perch	like ER, totally lacking red on breast
With Pale-headed	12.12.78	2	1	—	1	Palm Beach Qld.	perch	like PHR with faint red on head and upper breast, yellow lower breast, blue abdomen
Alone	13.6.78	2	2	—	—	Mt. Campbell 1 km SSE Piggabeen N.S.W.	perch	like ER dorsally, and PHR ventrally, extensive red on head
	11.5.79	1	1	—	—	Guineas Ck. Rd. 4 km W Currumbin Qld.	perch	like ER but lacking red on breast, blue/green breast and abdomen

ROSELLAS AND THEIR HYBRIDS

Of the 209 stops where rosellas were recorded during the survey eight or 3.8% included birds recognized as hybrids between Eastern and Pale-headed Rosellas (Table 3). Four of these observations included mixed species groups with at least one recognizable hybrid bird. One such group was a particularly large one for rosellas, consisting of approximately 35 birds sighted near Merrimac, some 6 to 7 km west of Broadbeach Queensland, on 13 April 1978 (the exact numbers of each species in the group could not be determined).

Within the area around Merrimac, two other hybrid groups were located at different times. Both Eastern and Pale-headed Rosellas were recorded consistently in this area throughout the survey period. Similarly both species were recorded in one of the other areas where hybrids were seen, namely Bonogin Creek. The remaining sightings of hybrids consisted of either hybrids seen alone or in the company of either Pale-headed or Eastern Rosellas. One hybrid was seen with an Eastern Rosella in the area of Bonogin Creek Queensland and one hybrid with a Pale-headed Rosella in the Palm Beach area of Queensland. The remaining two sightings of hybrids were of birds on their own. Two hybrids were seen in the Mount Campbell region of N.S.W. and a solitary bird near Currumbin in Queensland. In all cases hybrid birds were seen in open agricultural land.

DISCUSSION

Within the three habitats surveyed in southeastern Queensland and north-eastern N.S.W., Eastern and Pale-headed Rosellas were reasonably common, particularly in open agricultural areas. Crimson Rosellas were largely restricted to the forested areas which only comprised just over 10% of the habitats surveyed. This type of habitat is not as plentiful as the open agricultural areas in the region. Cain (1955) indicated that the range of the Crimson Rosella was probably more widespread in the past but long term climatic changes towards increased aridity (as well as more recent man-made alterations to the environment) have resulted in its range being restricted.

Eastern and Pale-headed Rosellas within the survey area were more common in 'open field' habitats created by land clearance. Keast (1961) suggested that, in contrast to the Crimson Rosella, the Eastern and Pale-headed Rosellas have probably extended their ranges as a result of man-made alterations to the environment until these two species now overlap. Certainly there was considerable habitat overlap between the Eastern and Pale-headed Rosellas in the survey area, to the extent that both species were recorded in the same area in over one third of cases (although birds were not frequently seen at the same time).

There is strong evidence that these two species are ecologically segregated, at least in some aspects of their feeding biology (Cannon, 1981), but the common occurrence of both species in the same area does indicate that the potential for interbreeding exists. Even though mixed species flocks were rare, nearly 4% of

flock sightings did include birds which were recognised as hybrids. The occurrence of wild hybrids (although not common), in areas where the ranges of the Eastern and Pale-headed Rosellas overlap, has been reported previously (see Keast, 1961; Forshaw, 1969). Short (1969) defined hybridization as the interbreeding of individuals of morphologically (and therefore presumably genetically) distinct populations, regardless of the taxonomic status of such populations. Using Short's criteria, the example of the Eastern and Pale-headed Rosellas is one of a zone of overlap and hybridization, rather than a hybrid zone *per se* where only hybrids occur. This zone of overlap probably results from secondary contact of the two species (Keast, 1961). The presence of hybrids in the wild, albeit rare, would indicate an incomplete development of isolating mechanisms (Ford, 1974). Members of the *Platycercus* genus hybridize readily in captivity (Forshaw, 1969). Eastern and Crimson Rosellas very rarely hybridize naturally (see Rogan, 1966; Courtney, 1967). This is probably because their habitat requirements are dissimilar, this being unlike the Eastern and Pale-headed Rosella in which their preferred habitats are similar.

Since the pair-bond of rosellas appears to be quite stable it must be assumed that mixed species pairs are formed within mixed species flocks (Brereton, 1971 a, b). Brereton (1971 b) indicated that pair formation of Eastern Rosellas occurs within small groups of 4 to 6 immature birds. These groups can form larger flocks during autumn and winter when they are less sedentary than pairs of breeding adults. The only large mixed species group of rosellas in the survey area was seen in autumn; most rosellas were sighted alone or as a pair. The opportunities, therefore, for mixed species pairs to form would be limited, despite the apparent considerable overlap of Eastern and Pale-headed Rosellas in the area.

Brereton & Sourry (1959) reported that the distribution of Eastern and Crimson Rosellas overlapped in the New England district of N.S.W. but mixed species flocks were very rare.

Nonetheless since the Pale-headed and Eastern Rosellas ranges overlap in south eastern Queensland and north eastern N.S.W. it is highly likely that mixed species flocks and even pockets of hybridization occur throughout this region. It would be interesting to continue to document the occurrence of such hybrids since they may prove to be more common than earlier evidence would indicate.

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Flock sizes of lorikeets, *Trichoglossus* spp.

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ABSTRACT

Flocks of Scaly-breasted Lorikeets *Trichoglossus chlorolepidotus* were generally larger, particularly when feeding, than flocks of Rainbow Lorikeets *T. haematodus* in south-eastern Queensland and north-eastern New South Wales. Although pairs of birds were the basic social unit, both species usually fed, flew and perched in flocks of less than five birds. Lorikeets, particularly Rainbows, congregated in much larger flocks (up to 1000 birds) at a permanent, artificial food source. Whether feeding at this food source or on naturally available blossoms in the surrounding area Rainbow Lorikeets associated in smaller flocks in late winter and spring, compared to other times of the year. Scaly-breasted Lorikeets did not exhibit such seasonal changes. Mixed species flocks were comparatively rare and were three to four times larger than the equivalent single species flocks. It is suggested that flocking, rather than territoriality, is probably a more efficient strategy for lorikeets which generally exploit temporary and shifting food sources, such as pollen and nectar of flowering trees and shrubs.

INTRODUCTION

Lorikeets are highly gregarious and are noted for their comparative tolerance between individuals during feeding, flying, roosting and nesting. Brereton (1963) suggested that they exhibited the highest degree of sociability of any Australian parrot. Forshaw (1969, 1973) reported that Rainbow Lorikeets *Trichoglossus haematodus* generally formed flocks of two to several hundred birds and Scaly-breasted Lorikeets *T. chlorolepidotus* were usually seen in flocks. Thus there are reports of some variability in the flock sizes of these parrots, although Walters (1979) indicated that the pair was the basic social unit in observed transit parties of *Trichoglossus* species.

To a large extent lorikeets exploit temporary food sources such as the pollen and nectar of flowering trees and shrubs (Churchill & Christensen, 1970; Cannon, in press a), the availability of which is variable in time and space. Evidence available suggest that the gregariousness of a species is largely related to the nature of its food supply and its predictability, i.e. some species feed in large flocks when

food is more scarce or less predictable (e.g. budgerigars (Wyndham, 1980a, b), *Quelea* (Ward, 1965), finches (Newton, 1967)). One would expect a certain variability in the sizes of lorikeet associations, depending on the predictability and availability of food.

This paper documents the extent of flocking of Rainbow and Scale-breasted Lorikeets in an area where the birds have access to a permanent food source, a mixture of diluted honey and bread provided at the Currumbin Sanctuary on the Gold Coast of Queensland.

MATERIALS AND METHODS

As lorikeets are high fliers and are very mobile, surveys were conducted by car in order to cover sufficient ground. The birds' noisy calls make it possible to detect them readily by sound. Two series of surveys were conducted in the Gold Coast and hinterland region of south-eastern Queensland and north-eastern part of N.S.W. to collect data on the diet and distribution of lorikeets in different habitats in the area (Cannon, in press a, b) and the sizes of lorikeet flocks. The first survey, conducted at two monthly intervals between March, 1978 and April, 1979, consisted of covering approximately 400 km of main and subsidiary roads with stops at approximately 2 km intervals (on each survey stops were within 50 m of each other). Thus there were about 200 spot observations per survey. The second series of surveys were conducted by car within a 5 km radius of the artificial food source at bi-monthly intervals from October, 1978 to August, 1979.

During each survey data were recorded on the sizes of single species flocks, the size and composition of mixed species flocks and the activities of these flocks (feeding, perching and flying). The term 'flock' is used in the sense of a loose association of birds rather than the term 'group' which according to Rowley *et al* (1979) has a definite membership over an extended period of time. Flock size was defined as the number of birds engaged in the same activity at the same time, other birds engaged in different activities were not included. The activities of a flock consisted of (a) birds feeding in the same or adjacent trees or shrubs, (b) birds perched in the same or adjacent trees or shrubs and (c) all birds flying provided they were travelling in the same direction with less than a 50 m spread. For relative frequencies of flock sizes, flocks were assigned to one of six categories following Brereton (1971 b) viz., 1-5, 6-10, 11-15, 16-20, 21-25 and greater than 25 birds.

Data on the number of lorikeets visiting the artificial food source at Currumbin were compiled from records of bird counts made at the same time of day during the morning and afternoon feeding sessions between March, 1979 and December, 1980. It is not known whether the same birds are present during both feeding sessions but other data (Cannon, in press b) indicate that some known banded individuals do return throughout the day. Since there was some

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indication from long term staff at the Currumbin Sanctuary that heavy rainfall coincided with large numbers of lorikeets at the artificial food source, rainfall data were obtained from the Brisbane Bureau of Meteorology and records kept at the Sanctuary from July, 1977.

RESULTS

LORIKEET FLOCKS WITHIN THE SURVEY AREA

Within the survey area both species were seen on a regular basis but not always in the same locality (Cannon, in press b). Rainbow Lorikeet flocks formed 66.9% of the total 1532 associations recorded and Scaly-breasted Lorikeets 27.9%. Only 80 records or 5.2% were mixed species flocks. Data on the mean flock sizes of single species flocks and the relative frequency of numbers within a single species flock of lorikeets during different activities are summarized in Table 1. Although the flock sizes of both species were quite variable the mean size was generally less than five birds, the mean number of 4.4 Scaly-breasted Lorikeets per flock being a little larger than that for Rainbow Lorikeets which was 3.7.

Rainbow Lorikeets tended to feed in small flocks, indeed over 90% of all Rainbow Lorikeets feeding flocks contained less than 5 birds. The data suggest that these birds tend to disperse when active, i.e., feeding or flying and congregate in somewhat larger flocks when perching and resting. The range of flock sizes were larger when these birds were flying, the largest sighted being a flock of 37 birds. Although Scaly-breasted Lorikeets were less frequently recorded in the

TABLE 1. Mean sizes and relative frequencies of single species flocks of Rainbow and Scaly-breasted Lorikeets when feeding, perching and flying.

Species	Activity	$\bar{x} \pm \text{S.D.}$ (range)	relative frequencies of flocks						Total No. birds	Total No. flocks
			1-5	6-10	11-15	16-20	21-25	>25		
Rainbow	feed	2.9 ± 2.5 (1-20)	91.2	7.9	0.4	0.4	—	—	651	226
	perch	4.7 ± 5.2 (1-30)	77.0	15.3	2.3	3.3	1.7	0.3	1365	292
	fly	3.4 ± 4.0 (1-37)	89.4	6.8	1.4	1.0	0.8	0.8	1736	507
									3752	1025
										3.7
Scaly-breasted	feed	5.4 ± 6.5 (1-50)	71.9	20.1	2.9	2.2	—	2.9	754	139
	perch	3.9 ± 4.8 (1-55)	87.1	11.2	0.6	0.6	—	0.6	664	170
	fly	3.9 ± 9.2 (1-100)	89.0	7.5	2.5	—	—	0.8	454	118
									1872	427
										4.4

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area the flock sizes of these birds when flying were somewhat larger than the Rainbow Lorikeet flock size, approximately 100 birds being the largest flock observed. Brereton (1971 b) indicated that at times parrot flocks increase and the largest were often feeding flocks. This was certainly the case with the Scaly-breasted Lorikeets which generally congregated in larger flocks when feeding than when perching or flying. Nonetheless closer examination of bird numbers in flocks shows that two birds are the basic unit for both species. The relative frequencies for groups of two birds are larger than any other category, irrespective of activity (e.g. Rainbow and Scaly-breasted Lorikeet respectively — feeding 39.8%, 26.8%; perching 45.0%, 52.9%; flying 38.9%, 41.5%).

The mean flock sizes of each species engaged in different activities in different months is shown in Figure 1. The Rainbow Lorikeets associated in larger flocks when feeding and flying during the summer and autumn but split into smaller flocks during winter and spring. There was less evidence of seasonal change in perching flocks of Rainbow Lorikeets although perching flocks during spring and summer were still slightly larger.

The flock size of Scaly-breasted Lorikeets when engaged in different activities showed a great range of flock sizes. Reference to Fig. 1 indicates a very marked increase in the numbers of birds feeding and flying together during May and June of 1978, a situation which was not repeated 12 months later in June, 1979. The mean flock size of Scaly-breasted Lorikeets seen feeding together during the period from May to August, 1978, was 10 and 11, which was the largest monthly mean recorded during the study. The largest feeding flock contained 50 birds which was seen during July/August, 1978. Flying flocks as large as 100 birds were seen during May and June, 1978 and the overall mean size of flying flocks was much larger at this time than at others.

Nonetheless the mean flock size of either species for all activities was five or less individuals, with the exception of the Scaly-breasted Lorikeet which fed in larger flocks of six to ten birds in March to October, 1978, and in Rainbow Lorikeets which occasionally perched in flocks greater than five in number.

MIXED SPECIES FLOCKS

Mixed species flocks were comparatively rare, only 5.2% of all flocks seen contained both species. The two species tended to associate more commonly when feeding; 71.3% of all mixed species flocks observed were feeding congregations (Table 2). Even when both species were seen feeding together they tended to remain segregated within a feeding station, that is pairs of the same species fed apart from pairs of the other species. Although the mean number of Scaly-breasted Lorikeets in mixed flocks was greater, 46 of the 80 associations contained more Rainbow Lorikeets and numbers of the former species in mixed flocks appeared to be more variable. Data were too few to ascertain whether there was seasonal variability in the composition of mixed species flocks.

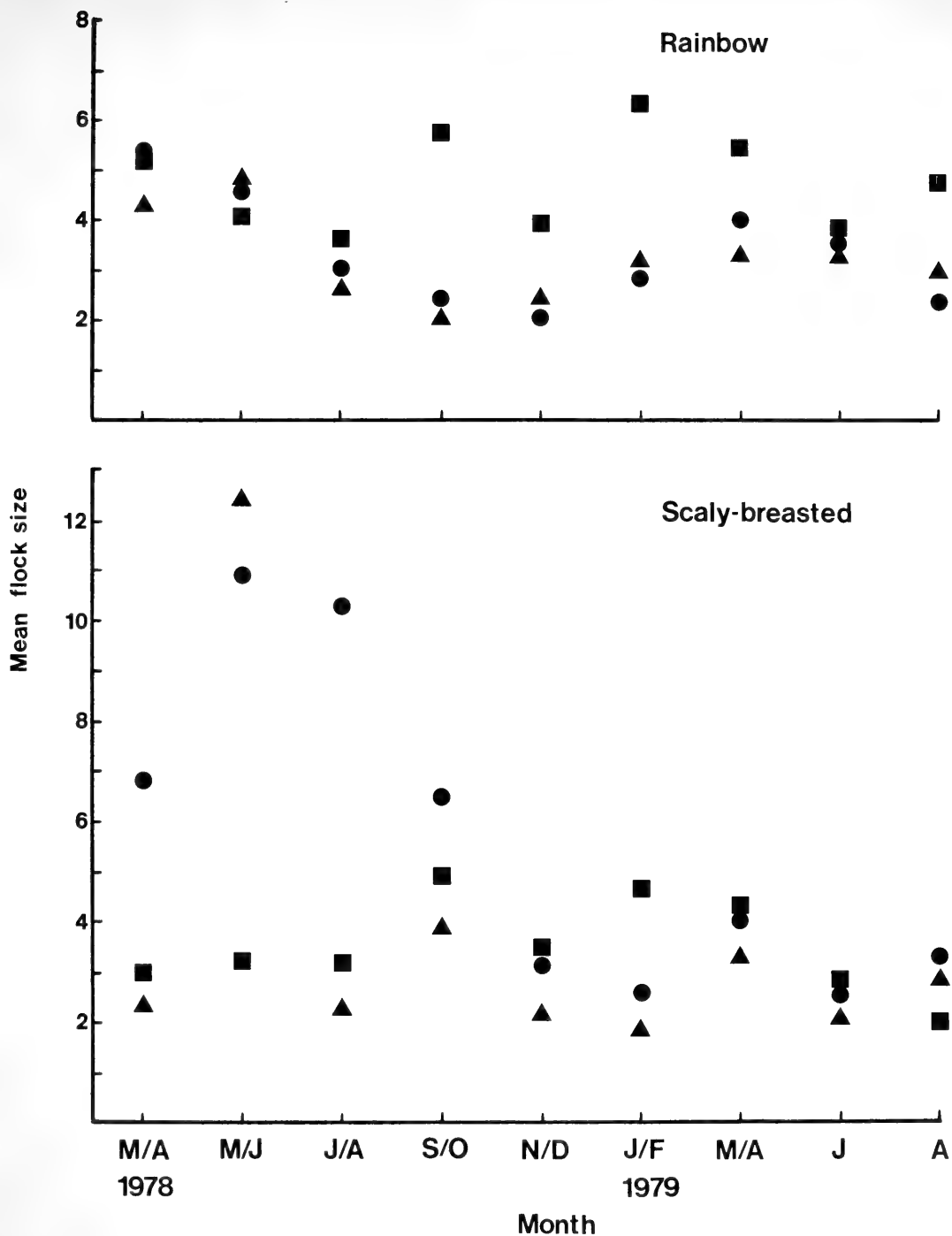


Fig. 1. Seasonal changes in the mean sizes of single species flocks of Rainbow and Scaly-breasted Lorikeets when feeding (circles), perching (squares) and flying (triangles).

TABLE 2. The mean sizes of mixed species flocks of Rainbow and Scaly-breasted Lorikeets when feeding, perching and flying.

Activity	Mean No. Rainbow \pm S.D. (range)	Mean No. Scaly \pm S.D. (range)	Mean No. mixed flock \pm S.D. (range)	Total No. birds	Total No. flocks	No. flocks with more Rainbow	No. flocks with more Scaly-breasted
Feed	5.9 \pm 6.2 (1-40)	6.9 \pm 7.5 (1-40)	12.8 \pm 11.8 (2-60)	732	57	32	25
Perch	5.7 \pm 4.9 (2-20)	6.4 \pm 7.5 (1-30)	12.1 \pm 10.5 (3-40)	170	14	8	6
Fly	6.0 \pm 4.3 (1-15)	7.8 \pm 7.6 (1-20)	13.9 \pm 9.5 (2-25)	125	9	6	3
Totals				1027	80	46	34
Mean No. birds per mixed species flock			12.8 \pm 11.2 (2-60) 80				

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LORIKEET NUMBERS AT AN ARTIFICIAL FOOD SOURCE

The large number of lorikeets, particularly the Rainbow, which congregated at the artificial food source were in marked contrast to the relatively small numbers of lorikeets which were observed elsewhere engaged in feeding and other activities. The mean number of lorikeets using the artificial food source daily (during any one month during a 20-month period) is shown in Figure 2 (derived from twice daily counts). Since Rainbow Lorikeets account for approximately 95% (\bar{x} 95.8, range 81.3-100, $N=100$) of birds using the food source the data are largely the numbers of this species using the food source. Some seasonal fluctuations in bird numbers are apparent. Fewer birds were seen in July and August compared with other times of the year, although there is considerable variation in bird numbers in any one month, for example the daily count of birds during March, 1980, varied between 12 and 800 birds. The maximum number of approximately 1000 birds was recorded during April and May, 1980 (which coincided with a period of heavy rain which washes the pollen and nectar out of flowers, the usual food

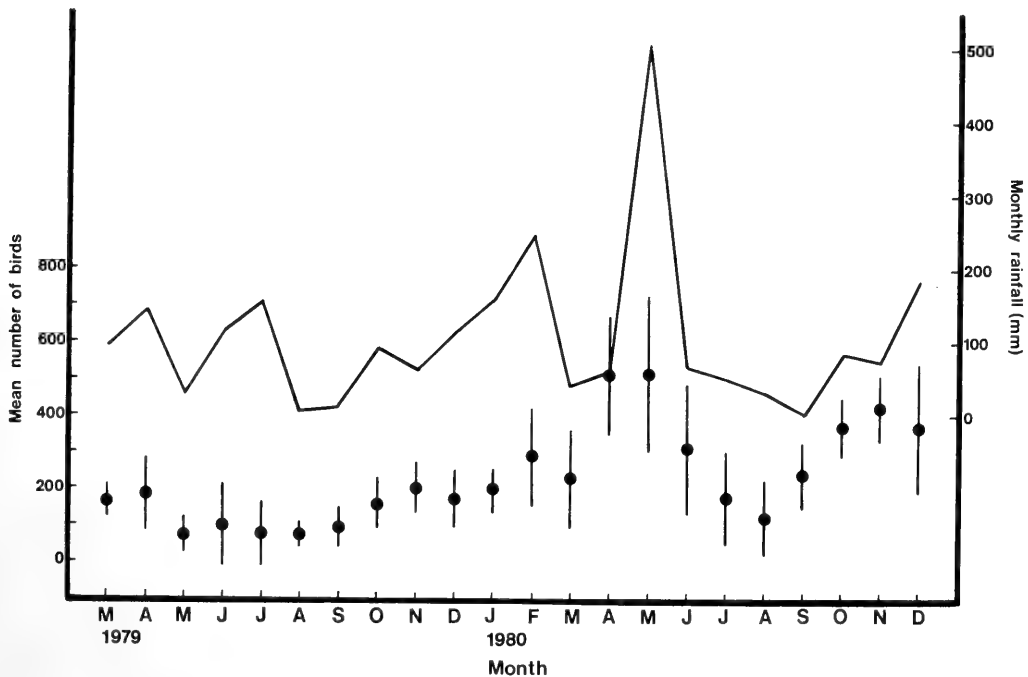


Fig. 2. The mean number of lorikeets using an artificial food source daily between March 1979 and December 1980. Circles show mean number of lorikeets attending the food source in each month (calculated from twice daily counts) and vertical lines the standard deviation. Monthly precipitation is graphed.

source of lorikeets). These numbers of birds are far larger than the sizes of feeding groups of Rainbow Lorikeets recorded away from the artificial food source, i.e., 1-20 birds.

OBSERVATION ON THE FEEDING BEHAVIOUR OF LORIKEETS AT ARTIFICIAL AND NATURAL FOOD SOURCES

Although both species were seen to feed from the same plate of artificial food it was not uncommon for the smaller Scaly-breasted Lorikeet to be displaced by the larger Rainbow Lorikeet which weighs approximately 40% more (Cannon, in press b). Indeed the Scaly-breasted Lorikeets often appeared to wait to feed until after most of the Rainbow Lorikeets had retired to perch in surrounding trees near the artificial food source. Only rarely did individual Scaly-breasted Lorikeets actively defend plates of food against individuals of the same species or Rainbow Lorikeets. This occurred more commonly with Rainbow Lorikeets.

When feeding on flowering trees and shrubs the two species tended to remain segregated in mixed species flocks, feeding in different parts of the tree or shrub. On rare occasions I have seen birds of either species actively chase birds of the same or the other species away from the particular group of flowers upon which they were feeding.

DISCUSSION

Lorikeets tend to be far more gregarious than many other parrots and anecdotal reports of large numbers of lorikeets gathering at a food source are common (see Bell, 1966, 1968; Forshaw, 1969, 1973). Indeed Brereton (1973) stated that this group of parrots are notable for the large size of their social groupings and for the comparative tolerance between individuals during feeding, flying, roosting and nesting. Nonetheless the data presented here confirms Walters' (1979) suggestion that the pair is the basic social entity in both Rainbow and Scaly-breasted Lorikeets. The average flock size of either species, whether engaged in feeding, perching or flying was generally less than five individuals throughout the year, and the most frequent associations were of two birds for both species. There was some seasonal variation in flock sizes, particularly for the Rainbow Lorikeet. This species tended to feed and fly in larger flocks during the late summer and autumn and occur in smaller flocks during the late winter and spring. There was less evidence of a regular seasonal pattern in the flock size of Scaly-breasted Lorikeets, although this species generally congregated in larger groups than the Rainbow Lorikeet, particularly when flying; perching groups of Scaly-breasted Lorikeets were larger in spring and summer.

Thus while only relatively small flocks of lorikeets were observed in the survey area during daytime the birds can form large night roosts. A temporary roosting flock of approximately 4000-5000 Scaly-breasted Lorikeets were seen over

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several days in an area near Southport Queensland approximately 20 km NNW of Currumbin during January, 1979.

In terms of the total number of birds seen in single species flocks Rainbow Lorikeets were more common than Scaly-breasted Lorikeets, forming approximately 67% and 33% respectively of the total number of birds seen ($N=5624$ birds in single species flocks). Within the survey area the two species were largely seen in different habitats, the Rainbow Lorikeet being more common in well vegetated urban areas and the Scaly-breasted Lorikeet in open agricultural areas (Cannon, in press a). Hence the rarity of mixed species flocks is not surprising. Only just over 5% of all flocks seen contained both species. Such flocks were generally three to four times larger than the equivalent single species flocks, irrespective of activity (whether feeding, flying or perching). Within all mixed species flocks the total number of Scaly-breasted Lorikeets appeared to out number the Rainbow Lorikeets, although more flocks had a greater proportion of Rainbow Lorikeets within them. Within mixed species flocks the two species, particularly when feeding, tended to remain segregated as monospecific pairs in different parts of a tree or shrub (see also Lavery and Blackman, 1970). Hybridization between the two lorikeet species has been reported (Cannon, in press b) but is uncommon.

Although Rainbow Lorikeets were somewhat more common in the environs of the artificial food source, that is Rainbow Lorikeets forming 67% and Scaly-breasted Lorikeets 33% of birds seen (Cannon, in press a) the former formed approximately 95% of the total lorikeets using the artificial food source. The implication is that the larger Rainbow Lorikeet (which weighs approximately 40% more than the Scaly-breasted Lorikeet) partially excludes the smaller Scaly-breasted Lorikeet. Fisler (1977) noted that species ranking at an artificial food source was basically determined by size, in addition Rainbow Lorikeets tended to be more dominant. Presumably the local Rainbow Lorikeets population use the artificial food source more than the local Scaly-breasted Lorikeets, although it is difficult to determine to what extent. Lorikeets of both species were seen to feed actively on an extensive range of flowering trees and shrubs in the local area (Cannon, in press a) and neither species appeared to experience noticeable food shortages.

The presence of larger numbers of Rainbow Lorikeets at the artificial food source during wetter periods of the year may be related to possible short term food shortages in as much as local heavy rainfall tends to result in lowered pollen and nectar availability. Staff members that have worked at the artificial food source over a period of years have noted that during periods of heavy rainfall the local lorikeet population use this food source more extensively. The main flowering periods which provides the major food sources for lorikeets appear to overlap sufficiently throughout a year to ensure a more or less continual supply of suitable flowering trees and shrubs. There is evidence that at least part of the local Rainbow Lorikeet population is largely locally nomadic (from banding studies —

see Cannon, in press b). Presumably when food is less available these birds may rely more heavily on the artificial food supply. At the present time the extent of the Scaly-breasted Lorikeets' mobility is unknown.

The relative absence of territoriality amongst birds which exploit a temporary food source is interesting. Generally lorikeets are noted for the comparative tolerance between individuals when feeding (and when engaged in other activities). Other birds of similar feeding habits, such as Australian honeyeaters, do exhibit varying degrees of territorial behaviour (Ford, 1979). Hamley (1977) noted a form of temporary territorial behaviour with pairs of Scaly-breasted Lorikeets. I have observed pairs of Rainbow and Scaly-breasted Lorikeets defending groups of flowers or plates of the artificial food but this is relatively uncommon. Territoriality as a strategy appears to be uncommon in lorikeets; generally a strategy of flocking is probably more efficient for these birds. Simplistically the chances of an individual finding food seems greater when that individual is a member of a flock, particularly when the food source is patchily distributed (see Cody, 1971; Murton, 1971; Ward & Zahavi, 1973).

Thus lorikeets seem to be relatively flexible, not so much in their main food source which are principally flowers but rather in the manner in which they procure their food. If necessary they can be highly gregarious in exploiting a range of foods.

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The rise and fall of the castaneous widgeon: an examination of the development of the binomial *Anas castanea* (Eyton)

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ABSTRACT

The development of the binomial *Anas castanea* (Eyton) is discussed. Historical literature concerned with the specific name, and the associated and confused synonymy, is reviewed, and some of the problems encountered by earlier authors examined in relation to the separation of what is now known as the chestnut teal from the grey teal *A. gibberifrons* (Müller). Early authors confused the two species, not appreciating the significance of size or plumage differences. They accepted uncritically various descriptions, which were occasionally based upon mis-sexed individuals, they had no understanding of specific ecology, dispersal or local distribution patterns, and others too were prepared to sustain views incompatible with available data.

Increasingly, towards the end of the nineteenth century, the matter was reaching resolution but well into this century some attempts were made to recombine *castanea* with *gibberifrons*. The late recognition that *punctata*, a synonym used by Gould and other authors, was an African species in no way associated with the Australian teal, and the involvement of numerous other species, indicates the complexity achieved by successive, even competing and contradicting taxonomists. One unfortunate consequence of this melange locally has been the almost total confusion within early distribution records, and hence an inability to establish accurate historic ranges.

I am quite ready to disclaim the credit of authorship, if it can be conclusively shown that any of my so-called new species are invalid, for I have . . . but one object in view, namely, the advancement of Ornithological Science. But I have a right to examine the data on which any adverse opinions are founded . . .

W. Buller (1869b).

INTRODUCTION

In 1983 the Royal Australasian Ornithologists Union (RAOU) will produce the fruits of the past five years labour. Within the forthcoming *Atlas of Australian birds* the Union will present, where appropriate, past and recent (to 1981) distribu-

tion records of over 650 species, collected by more than 2600 observers all based within a grid network of 1° by 1° (Royal Australasian Ornithologists Union 1982). In the presentation, the *Atlas* will inevitably continue one of the problems inherent in such publications, the inclusion of some undetected, perhaps undetectable, errors. Repetitious records will dilute most faulty observations and many of the recent sightings can be compared with each other and be discussed amongst observers. Whilst apparently spurious observations can be removed, historical records from manuscript, literature or museum sources may present a further problem which may not always be effectively eliminated. Certainly, for most species resolution may come by consideration of past and present ranges, with isolated, extra-limital records being excluded. However, series of such records complicate matters which are magnified when sympatric, apparently similar species are concerned, particularly when the separation of such conspecifics is delayed, contradicted or denied.

This review details some aspects of the development of the specific binomial for what is now known as the chestnut teal *Anas castanea*, examines the previously, often confused relationship between *castanea* and the related grey teal *A. gibberifrons*, and discusses some of the problems encountered by those dealing with the species involved.

THE RISE OF THE CASTANEOUS WIDGEON

In 1803 officers and crew of the *Calcutta* were in Port Phillip Bay, Victoria, as part of an expedition to establish a settlement within easy reach of Bass Strait. During the course of operations one of the officers, First Lieutenant Tuckey, described elements of the local fauna. As with other early visitors to coastal regions of the continent (for some other examples see Whittell 1954) Tuckey discussed some of the waterbirds of the district, including a 'teal of a beautiful plumage' (Tuckey 1805). Some years later, in Africa, Burchell recorded a small brown duck known locally as a widgeon which, almost casually and in footnote, he named *Anas punctata* (Burchell 1822). From such trivial, disparate beginnings were the origins of confusion and debate which surrounded the taxonomic maturation of what is now known as *Anas castanea*.

In 1838, T. C. Eyton published his monograph on the duck tribe in which was described a new species, the castaneous widgeon *Mareca castanea*, a bird which inhabited New Holland (Eyton 1838). In the relatively brief description, and associated plate, there is sufficient detail to demonstrate clearly that Eyton recognised that the male and female had dimorphic plumages. However, shortly afterwards, John Gould (1845) considered that the chestnut-breasted duck, *Anas punctata*, Cuv., which was 'universally diffused over the southern portion of Australia . . . (and) in some parts of Van Diemen's Land', was synonymous with *M. castanea*. In this Gould followed, apparently, Gray (1844), who had attributed the specific designation to Cuvier though without detailing the source. However,

in the version of *Le règne animal* published in 1829 it was noted that *A. punctata* was first described by Burchell in his *Travels* (wrongly given as 1811, Cuvier 1829): perhaps this represented Gould's source, and the source of others.

Gould (1848) considered that the species was 'nearly allied' to the true ducks *Anas*, and provisionally placed it with them. In his original description of the species (1845), he noted that the male was rarely seen in the nuptial dress, of a rich, deep and changeable bronze-green head and neck. The distinct plumage, adopted in the spring, was Gould thought only assumed when the bird was two or three years old, and he considered that the male and female plumages were similar for at least nine months of the year. However, Gould (1865) later modified his views, and suggested that since there were large size differences there might be two races — indeed 'the idea presents itself of their being really distinct species', with the smaller birds being found in Tasmania, the larger in western and southern Australia. J. Cotton, who was preparing a series of sketches of Victorian birds shortly after Gould had started production, clearly indicated a male 'mountain teal' [pl. 28, sketch book 2; see McEvey 1974] with a green head. Cotton too, in his posthumously-published work, had noted [pl. 29] the red iris, an age character missed by Gould and, obviously, unavailable to Eyton. Identifying it as *A. punctata* Cotton was but unwittingly keeping company with other contemporaries such as Lichtenstein (1854) who, placing it within *Querquedula* (teal), gave its range as New Holland. MacGillivray (1852) recorded *punctata* from northern, tropical Australia and Gray (1858, 1859a) on the other hand gave its distribution as from north Australia to 14° S., Port Essington and Cape York as well as from New Caledonia, or at least he recorded a variety as coming from there; Gray also noted that there were problems in further identification. Whilst some collectors operating locally, for example within Bass Strait, were obtaining wild duck and identifying them as *Anas punctata* Cuvier (Denham 1858), a man with perhaps more practical and intimate experience with local waterfowl, recognised that both the male and the female had distinct plumages and he 'always considered it a distinct variety, which some of the old duck-shooters also did' (Wheelwright 1865). Interestingly he recorded shooting 'a dull-coloured bird with a red eye, which, on dissection, proved to be a male.' But by 1871 Gray had reintroduced *punctata* back into *Mareca*, extending its range from New South Wales, western Australia and Van Diemen's Land, to the Molluccas and New Caledonia (Gray 1871), even though he had earlier (Gray 1858, 1859a) voiced some uncertainty about the specific identity. And, as an example of the continuance of a dubious record, Marié (1870) listed *Mareca castanea* (Gould) as being a member of the New Caledonian avifauna, attributing the record apparently to Gray who had recorded '*Anas punctata*, (Gould?); var.' from there years before (Gray 1859b). However, Wallace (1863) retained *Anas*, and recorded *A. gibb(er)ifrons* from Timor. Eyton (1869) too appeared to have ignored other revisionary authors, including Gould and continued with *M. castanea*. And meanwhile Burchell's small brown duck continued, almost ignored, in a footnote.

Matters took quite a different direction after Alfred Newton examined some specimens of Australian ducks which had died in the Zoological Society's Gardens. In his discussion of the specimens, Newton (1871) clearly showed (in a footnote) that there were indeed two 'perfectly distinct species (which) have had the name *Anas punctata* applied to them'. Newton discussed the synonymies further, noting that Pucheran (1850) had identified the specimen in the Paris Museum with the description of *A. punctata* presented by Gould. Lesson (1831) had previously recorded such a species (which he described as 'Tête et cou noirs; plumage roux') from Java in the 'Gal. de Paris', suggesting that it might be one of Horsfield's specimens. Lesson, though, had not provided an author for the binomial. Since Newton felt that it was uncertain where and when Cuvier had published the name *punctata*, he suggested that *punctata* should be retained for the South African bird recently redesignated as *Querquedula hottentotta* by Smith (1845). Certainly Gray was, according to Newton, unable to recollect where he obtained information concerning Cuvier's description. Accordingly Newton considered that the Australian bird should 'take up with its next synonym - . . . *Anas castanea* (Eyton)'.

But having established the apparent chain of events, and determined an appropriate binomial, Newton re-assigned the Australian duck to a new genus *Virago*, a consequence of a supposed female having a tracheal structure usually restricted to males (bullae osseae). Whilst 'averse to inventing new groups', Newton anticipated that the apparent singularity of his birds would lead to the designation of them as the type of a new genus or subgenus, and felt that *Virago* was appropriate 'as a tribute to the virile characteristic of the ladies in question'. This proposal was too late apparently for inclusion in Giebel's (1872-77) thesaurus, where *punctata* — from 'Australia merid. Tasmarina' — was recorded as a synonym for the *Mareca castanea* of Eyton and *M. punctata* of Gray; Burchell's *punctata*, from 'Africa merid.', was also noted. The genus *Virago* was also ignored by Reichenow (1882), who listed *A. castanea* Eyt. as having 'Kopf und Hals glänzend grünschwarz; Kropf und ganzer Unterkörper rothbraun . . . Weibchen hellbraun', and gave its range as Australia. *A. punctata* was recorded from the Port Denison region by Ramsay (1866) and he still retained *A. punctata* when listing game species and other birds requiring protection in New South Wales, including all Australia within its distribution (Ramsay 1877). However, in 1878 Ramsay combined *A. punctata* Cuv. with *Anas* (*Virago*) *castanea* Eyton and showed the species' range as including southern New Guinea, most of Australia including the interior, but not Ports Darwin or Essington, the Gulf of Carpentaria or Cape York (Ramsay 1878a). Shortly afterwards Ramsay (1878c) contradicted Newton's findings, noting that he had not found any bullae osseae in females of *Anas castanea*, 'our common Australian Teal'. Ramsay suggested that Newton had, in fact, been misled by the carelessness of a taxidermist, a point which Newton (1871) had taken pains to dismiss.

Whilst Müller had apparently recognised that *Anas* (*Mareca*) *gibberifrons* was distinct from *Mareca castanea*, and commented on the similarity of the specula

('even als bij *Mareca castanea*, Eyton'), Ramsay (1878a) sought records of *Anas gibberifrons* which Müller (1842) had recorded from the Celebes; the species was said 'to have been obtained in both North and South Australia,' though Ramsay thought that it was 'very improbable'. Buller (1869a) had earlier described the species from New Zealand, as *A. gracilis*, though he was later to accept that it was in error (Buller 1869b). Indeed Finsch (1869), commenting on Buller's article which had included reference to *A. gracilis*, noted that it was identical to *gibberifrons* which had 'a wide geographical distribution' including Timor, Flores, Celebes, northern and South Australia, as well as New Caledonia. Ramsay (1878b) also examined a specimen of *gibberifrons* from New Zealand and, though noting that it was somewhat smaller than female or young male *castanea* from New South Wales, dismissed the variation as being related to sexual or individual difference. Though in this species the male plumages were said to resemble those of females, Ramsay considered that the matter had not been satisfactorily resolved. Indeed he (Ramsay 1878b) further demonstrated the current dilemma and uncertainty when he noted that it was rare 'to obtain adult males in full plumage', and he felt that when the 'breeding places' of the New Zealand birds were found 'adult males in the summer plumage, resembling that dress of the N(ew) S(outh) W(ales) birds, may nevertheless be procured.' Hutton (1880) also added to the confusion by suggesting, again, that *gracilis* was distinct from *gibberifrons* but worse, that *gracilis* was a synonym of *castanea*.

Sclater (1880b), in discussing species of anatids introduced into the various zoological gardens of Europe, mentioned *A. castanea* (Eyton), the chestnut-breasted duck of Australia, and obviously considered it to be a synonym of *A. punctata* of Gould, and *Mareca castanea* of Eyton. Sclater listed the species separately from Müller's Duck *A. gibberifrons*, which ranged from the Celebes and Moluccas, to Australia and New Zealand, and noted too that the birds previously considered to be *castanea* were in fact *gibberifrons* 'which much resembles the female of *A. castanea*'. In his listing Sclater considered that *A. gibberifrons* was the synonym of *Querquedula gibberifrons*, *A. gracilis*, and *Mareca albigularis*, and he recorded *A. chlorotis* as a separate species from New Zealand. But shortly before Sclater (1880a), again discussing birds registered at the Zoological Society as *A. punctata* (*castanea*), had not found the anticipated full breeding plumage as described by Gould. He felt that the birds had, in fact, been *A. gibberifrons* 'a species closely resembling the female of *A. punctata*, which has lately been ascertained to occur in Australia!' Salvadori (1895) was also 'utterly unable' to distinguish between the females of *Anas castanea* (listed as *Nettion castaneum*) and *gibberifrons* despite the fact that he had earlier (1880-1883) noted that the female *castanea* greatly resembled both the male and female *gibberifrons*, but it was bigger.

Sclater (1882) added some further comment on the taxonomic confusion. *A. gibberifrons* was, he considered, quite distinct 'however much it may resemble the female of *Anas castanea*', and he repeated that it was the same species described as *A. gracilis* (Buller 1869a) but later identified as *A. gibberifrons* (Finsch 1869).

Certainly, said Sclater, Hutton's (1880) unsupported opinion that *gracilis* was distinct from *gibberifrons* could hardly be accepted. And, in attempting to reduce matters to some sensibility, Sclater dismissed Newton's (1871) proposal of *Virago*, for he felt there was 'little doubt' that the presumed female had 'in all probability' been a male *A. gibberifrons*. He noted, too, that the bill of *castanea* was longer and larger than that of *gibberifrons*. But this rejection was seemingly ignored by Stejneger (1885), who continued with Newton's genus *Virago* and still attributed *bullae osseae* to the female. Blasius (1883) too, quoted Reichenow who considered that 'Mit *Anas punctata* ist *castanea* Eyt. gemeint', and Broinowski (1887), when discussing *A. punctata* (Cuv.), still raised the question as to whether two distinct species existed. Broinowski noted the similarity of male and female plumages *except* in the breeding season (following some earlier authors), and felt that the Tasmanian birds were generally smaller than those on the mainland. Nevertheless, by 1887 Ramsay at least had apparently accepted both *A. castanea* and *gibberifrons* (Ramsay 1887), and he gave the distribution of the former as Derby, north western Australia; Rockingham Bay, Port Denison, Wide Bay, New South Wales, Victoria, South Australia, Tasmania, west and south Western Australia; *castanea* was not found in the interior whereas *gibberifrons* was (Ramsay 1888). Ramsay also mentioned the possibility of *Anas gibberifrons* in southern New Guinea but considered it to be absent from Tasmania and west and south Western Australia. And some further assistance in the clarification of the binomial *Anas castanea* was the repetition by Tristram (1889) that *punctata* of Burchell was indeed from the Transvaal, and was quite separate from *castanea* and *gibberifrons*, the latter being represented by a specimen from East Timor.

North (1889), however, still showed that there was uncertainty about the species, and their respective merits. In repeating Ramsay's (1888) distribution for *A. castanea*, he then reported eggs of that species from the interior of New South Wales and included *A. punctata* Cuv. as a synonym. Nevertheless, *gibberifrons* was reported by North as a species which had been recorded from New Zealand under the name of *A. gracilis*. Somewhat belatedly, Stirling (1890) joined earlier authors and 'exhibited a specimen of teal of brilliant plumage of rare occurrence, *Anas castanea*.' But he disagreed with the earlier comments, made for example by Gould, that such a plumage was merely the nuptial dress: indeed he felt it was a distinct species. And Keartland (1890a) also added his comments on the matter. The Field Naturalists Club of Victoria had been on a trip to King Island where some male *Anas castanea* were shot. Since, said Keartland, it was generally known that teal breed in the close season (i.e. not open to hunting, 1 Aug. to 20 Dec.) then no 'beautiful birds' should be in collections. However, there were and as such it 'conclusively proves that the change of plumage theory is an error.' The common sombre birds were mainly from the Murray flats whilst the gay birds were from Gippsland; indeed said Keartland one 'must go to the hilly districts to find the chestnut-breasted ones'. Keartland (1890b) had further noted that sombre birds had been shot on King Island and upon dissection four proved to

be adult males — they were not females of the chestnut-breasted variety, which was in apparent contradiction to Campbell's (1890) proposal that the 'sombre' birds were, in fact, female chestnut teal.

Whilst *Anas punctata* Cuv., from Australia, was still in use in some publications towards the close of the nineteenth century (e.g. in a catalogue of a collection, Hartert 1891) there was no doubt that Salvadori (1895), when discussing the collection of skins held by the British Museum, recognised that there were two species — the problem which remained unresolved was what specimens or records had earlier authors considered to be, and included as, *Nettion castaneum* and what as *N. gibberifrons*? (The use of *Nettion* was a consequence of changing nomenclature for the group of ducks known as teal). Salvadori (1880-1883) thought that records of *castanea* from southern New Guinea were probably *gibberifrons*, as were those from New Caledonia and Java. Indeed he also suspected that a specimen in the Paris museum, labelled *A. punctata* and said to have come from Java, was also *gibberifrons*; and felt that one of Verreaux' specimens in the Leiden Museum, from New Caledonia, though labelled *castanea* was in fact *gibberifrons*. Thus he (Salvadori 1895) summarised the range of *castaneum* as including Australia, New Zealand, questionably New Caledonia, and considered it to be a straggler in Java and the Celebes, and Sharpe (1899) also included New Zealand in its distribution.

Meyer and Wigglesworth (1898) discussed the problem further and concluded that the evidence that *castaneum* and *gibberifrons* were separate and distinct species was satisfactory and that there was 'no sound evidence to show that *N. castaneum* has ever occurred outside of Australia and Tasmania.' Indeed, they noted that Ramsay had reduced his claim for the species' range (see above), and they suggested that the earlier records of *Anas punctata* var. (Gray 1859a, Verreaux and des Murs 1860; see also Schlegel 1866, Jouan 1863) from New Caledonia were incorrect, referring probably to *Nettion gibberifrons* (see also Walden 1872). They also thought that Salvadori's record of a female *castaneum* from New Zealand was in error particularly since he had admitted an inability to distinguish females of the two species (Salvadori 1895). Meyer and Wigglesworth (1898) also considered *Mareca punctata* (= *N. castaneum*) recorded by Meyer (1881) from Sumba to be identical with their birds from the Celebes, i.e. *Nettion gibberifrons*. Lesson's (1831) record of *Anas punctata* from Java was also disregarded since Meyer and Wigglesworth thought that the authority (? Horsfield) was doubtful, and Reichenow's (1877, 1883) reports were also dubious, though *gibberifrons* had been recorded from the region. Indeed Reichenow had indicated that the specimen was a female, which might be *gibberifrons* 'if that species is distinct' (Meyer and Wigglesworth 1898)! They noted too that the *Anas punctata* Tem. of Finsch (1865) had been placed under *Dendrocygna guttata* (a tree duck) by Salvadori, 'apparently with perfect right.'

Locally Campbell (1901) also pursued the problem but felt that there was 'no doubt about the existence of this second variety of Teal in Australia', and

as proof he pointed out that Keartland had found that female chestnut teal were almost a third heavier than the grey teal, 'evidence that seems to speak for itself.' Leach (1908) too, who recognised that both *Nettion castaneum* and *gibberifrons* occurred in Victoria, stated that the former was heavier; Hall (1906) on the other hand gave some specific differences in distribution but noted, perhaps as an error of transcription, that the male *gibberifrons* was two inches longer than the male *castaneum*. Littler (1910) also provided regional information, and considered that *castaneum* was 'scarce' in Tasmania, or 'at least the males are but seldom procured', whereas *gibberifrons* was found throughout Australia, New Zealand and on a number of islands to the north. In attempting to clarify his observations on the species Littler included comments from Campbell. Littler apparently believed that 'many males breed before they have attained full livery', but once attained it was not lost, and Campbell also considered that the black (*sic*) head and neck were retained during the non-breeding season in *castaneum* whilst *gibberifrons* was permanently monomorphic. North (1913) again discussed the confusion between the two teal species, resurrected *Nettion*, and gave a more extended distribution for *castaneum* which included the north-west, Northern Territory, and Queensland. North considered the species' stronghold to be southern Australia, the islands of Bass Strait and Tasmania, essentially coastal, whereas *gibberifrons* (not recorded from Tasmania by North) was more of an inland species. However, in his commentary North included remarks of Carter who had apparently shot a female teal in male plumage — was this too, like Newton earlier, an error of dissection?

Whilst some Australian observers were reaching a confused form of consensus, the situation was not improved by Sassi's (1909) attempt to include *Anas chlorotis* into the North Queensland avifauna. Whilst the white base to the under-tail coverts and white collar were absent from the birds in question, the green 'Schimmer' was present on the juvenile male, according to Sassi. Presumably the specimen was an adult male *A. gibberifrons* as was the apparently stained bird from north Queensland, listed as *Querquedula (Nettion) castanea*.

Gregory Mathews, who was to consolidate (according to his standards) the systematics of the Australian avifauna, was responsible for considerable manipulation and re-arrangement of families, genera and species. At times a taxonomic 'splitter' of no mean proportion, particularly where genera were concerned, Mathews was thought by some to have seriously affected the later development of local ornithology (see Serventy 1950 for some details). Certainly he revised, modified and frequently re-named species, and with changing purpose, and in so doing affected the contemporary view on the nomenclature of the local teal species, along with other waterfowl. Thus in his handlist of Australian birds Mathews (1908) accepted *Nettion castaneum* as ranging throughout Australia generally, including Tasmania, and apparently thought that it occurred in New Zealand, Java and the Celebes. *N. gibberifrons*, on the other hand, he thought, was distributed, outside Australia, in New Guinea, the Celebes, Sunda and New Zealand.

And shortly afterwards he reported the extra-limital occurrences of both *Nettion castaneum* and *gibberifrons* (Mathews 1912a). In his devotion to trinomialism, Mathews (1912b) described a new subspecies *N. c. rogersi*, the western teal, from north-west Australia and the Northern Territory, which was distinguishable from the adult female of *N.c. castaneum* 'in being considerably lighter on the head and back; and in having the centre of the feathers of the under-surface not so dark' (see also Mathews 1913). However, in his 1913 list (Mathews 1913), *castanea* had rejoined *Virago*, a genus not in vogue for some time following dispute regarding its validity (e.g. Ramsay 1878c, Sclater 1882). Mathews included Queensland within *castanea*'s range and continued to advocate the subspecies *rogersi* — the western teal from Parry's Creek. Whilst the generic association was continued in his volumes devoted to the birds of Australia (Mathews 1914-15), the author admitted that the 'confusion' between *Virago castanea* and the now *V. gibberifrons* had 'not yet been unravelled' to his satisfaction. Furthermore, and importantly, he accepted that the ranges and life histories of the two species had been thoroughly confused. So too was the terminology used in his book, for the plate of *gibberifrons* was labelled *Nettion rogersi* whilst the text gave *V.g. rogersi*, and the plate of *castaneum* was revised in the text to *V. castanea*. And, almost in passing, Mathews noted that the nestling of *castanea* was 'much darker than that of "*gibberifrons rogersi*"' now included without comment as a synonym for *Virago castaneum rogersi*, and placed within *gibberifrons*. He did, though, consider that his earlier 'disposition' was not confirmed by additional material and was 'compelled to admit that I cannot yet confidently assert that I know all about these birds and their inter-relationships.' He proposed, therefore, that his conclusions were 'of a tentative character only.' Indeed he went on to provide further evidence of his own confusion, and that of others. Thus in a listing of New Zealand birds, Mathews and Iredale (1913) thought that *N. castaneum* included *gracilis* and *gibberifrons*, and noted that they were not satisfied that *gibberifrons* occurred either in Australia or New Zealand. Indeed they felt that the only New Zealand specimens available 'undoubtedly' belonged to *castaneum*. According to Mathews (1914-15), it was quite possible that collectors had been 'carried away by the belief that only the male had a green head', and whilst discussing *Virago gibberifrons* he suggested that *Nettion castaneum* (sic) '*has the male and female alike in coloration when adult*' (Mathews' italics), a novel attempt indeed to reconcile apparently contradictory earlier records and observations including records of green-headed birds sexed as females. Mathews also included considerable mention of an article by White (1914), which he felt he had stimulated. Certainly White had few doubts on the subject, for he felt that there was 'not a shadow of doubt' that there were 'two distinct species, and good ones at that.' White indicated that the Eastern Teal, Mountain or Chestnut-breasted Teal was heavier and less common than the 'grey species' and he suggested that their different habits, and the absence of chestnut teal in areas where grey teal were breeding 'surely . . . must dispel any doubt upon the subject.' Mathews too, in his discussion on *gibberifrons*, noted that the 'green-

headed bird is strictly southern' whilst 'the other species goes all over Australia and Tasmania and is the only species found north of the Tropics'. But, despite some mention of the variability of bill size whilst discussing measurements in *V. gibberifrons* (Mathews 1914-15), a new subspecies of *castanea*, *V.c. alexanderi*, was unabashedly described (Mathews 1916a) as 'having a smaller, narrower bill' than *V.c. castanea* (Eyton), and repeated (Mathews 1916b) as an alteration to his early list (see also Mathews 1920, 1927). And further, in an article on birds on a lake in Western Australia, Mathews was to note that though a female *Virago castanea* was just assuming a chestnut breast it 'had no green on its head or neck' (Carter and Mathews 1920).

For a while, perhaps surprisingly, the debate was to be continued. Belcher (1914) considered that, in his opinion, 'the evidence, conflicting as it is, does not warrant our recognising more than one species', though he noted that shooters on Lake Connewarre certainly recognised two birds. Alexander (1916), in an endeavour to identify some specimens, weighed some birds and compared his results with earlier details. He concluded that all his (unsexed) birds were grey teal, including green-headed birds, and like others before him wondered whether both species sometimes assumed the chestnut and green plumage. However, Alexander did note that he had sexed a green-headed bird 'which proved to be a male'. On the other hand Blaauw (1916) disagreed with Mathews' proposal that both sexes of *Nettion castaneum* were alike in plumage, since he had bred the species for some years, and had found that the male and female plumages were distinct. He had also noticed that young males began to adopt adult plumage when some five or six months old. And for some time the separation of the two species was readily accepted, with observers (e.g. McGilp 1923) and compilers (e.g. Lord and Scott 1924) placing them within *Virago*, whereas the official view given in the *Checklist* (Royal Australasian Ornithologists Union 1926) included the species within *Querquedula* (noting that *Virago* was a subgenus). Such placements were in contrast with the views of Phillips (1923) who included *gibberifrons* and *castanea* within *Anas*. Phillips mentioned too that there had been some earlier confusion but felt that the species did not occur outside Australia, 'and possibly New Zealand' whilst records to the north of Australia were referable to *A. gibberifrons*. He also stated, following Blaauw and others, that female *castanea* never (except perhaps for pathological reasons) assume the male plumage. In enumerating the specific differences between *gibberifrons* and *castanea*, Phillips referred to a 'bony frontal knob found in all old male specimens of the Gray Teal.' However, he noted that of 28 males he had examined from the Celebes only six or eight were easily distinguished by that character. Phillips also considered *Nettion castaneum rogersi*, earlier recognised by Mathews (Mathews 1912b): since *rogersi* was previously used in combination with *Anas superciliosa* then it became redundant once *gibberifrons* was moved from *Virago* (or other genera) into *Anas*. In consequence Phillips proposed that *mathewsi* be its new trinomial. Hartert (1931) too, in examining the Mathews' types held in the Tring Museum, also considered

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that, even if *N.c. rogersi* was valid, it was a junior synonym of *A. gibberifrons gracilis*, described by Buller (1869a) forty-three years previously.

Despite a reasonable consensus of opinion, that the two species *gibberifrons* and *castanea* really were distinct and had differing ranges, Ripley (1942) introduced a new dimension in the development of the nomenclature of what was once known as the castaneous widgeon. In his review Ripley proposed the recombination of *gibberifrons* with *castanea*, claiming that both had a 'curious frontal-sinus enlargement'. Within the subspecies *A.c. castanea* he included *V.c. alexanderi* of Mathews (1916a); *A.g. mathewsi* was accepted as *A.c. mathewsi*, distinguishable 'on the basis of generally smaller proportions.' Having rejoined the two species, Ripley then commented on the distinct ranges of the two subspecies or 'forms' (with *mathewsi* being northern), discussed mechanisms which might have resulted in their contrasting plumages, and noted that there were reports of apparent overlap in distribution. In addition a new subspecies, *A.c. remissa*, was proposed by Ripley for a small duck from Rennell Island in the Solomons. *Gibberifrons* was relegated to a subspecies of *castanea* on the basis of the enlarged frontal bones, which was not restricted only to males (cf. Phillips 1923), a feature previously given, apparently, for the species itself. Ripley also accepted two other subspecies of *castanea*, *albogularis* and *leucopareus*, though with some qualifications. However, as Jones (1942) was quick to point out, Ripley made no mention that *A.c. mathewsi* (= *A. gibberifrons*) was the commonest species in southern Australia. Jones dismissed Ripley's views on the aberrant plumage of *A.c. castanea*, and Mathews (1946), who was still maintaining *gibberifrons* and *castanea* within *Virago*, ignored them: other authors (e.g. Terrill and Rix 1950) kept the two species within *Querquedula*. Delacour (1956) too, when reviewing the waterfowl of the world, considered that there were still two good species and returned some of Ripley's subspecies to *A. gibberifrons* which, in turn, he felt was closely related to *A. bernieri*, *A. castanea* and *A. aucklandica* — the austral teal group.

Though many authors had earlier recognised that the *Anas punctata* of Burchell (1822) was not in fact anything to do with the austral teal *gibberifrons* and *castanea*, it was not until Ride and Cain (1954) examined one of Burchell's specimens that it was realised that the skin was of *Erismatura maccoa*, a stiff-tailed duck known as the Maccoa, and should represent the type named *A. punctata*. Since this discovery presented considerable nomenclatural problems they proposed that the matter be maintained *sub judice* until resolved. Ride *et al.* (1956) subsequently sought the approval of the International Commission on Zoological Nomenclature to preserve the binomial *punctata* as the specific name for the Hottentot teal. Technically, though *punctata* should have been applied to *maccoa*, the authors considered that if the rules of nomenclature were rigidly applied serious confusion would ensue. Ride *et al.* suggested a series of procedural manoeuvres which ensured retention of *punctata* within the discretionary powers of the Commission. Thus they recommended the suppression of the name *punctata* as used by Lesson (1831) 'for the Australian duck named *Mareca castanea* by Eyton'.

They considered that *punctata* had originated from a manuscript label of Cuvier's on a male bird in the Paris museum. Ride *et al.* commented on the erroneous use of *punctata* by Finsch (1865) for *Dendrocygna guttata* and discussed the early application of the specific name *albogularis*. In considering that Sclater (1880b) had provided the first 'clearly satisfactory usage' of *Anas punctata* for the Hottentot teal they noted that they had had to review the synonymy of five other species. According to Serventy (1956), the strict application of the laws of priority would defeat such a complex proposal; however, an increased flexibility was current and it was somewhat easier, apparently, to reject earlier specific names. Nevertheless, differing opinions on the proposal of Ride *et al.* promoted disagreement and it did not reach the voting stage. Ride (1974) again sought the suppression of *punctata*, and the acceptance of *hottentota* and *maccoa* as published by Eyton (1838). This proposal was accepted by the Standing Committee on Ornithological Nomenclature of the International Ornithological Congress (Eisenmann 1975). Even though some objectors considered it quite inappropriate to substitute a type of a different species when the actual type was available (see Ride 1974, Eisenmann 1975), the proposal was accepted (Nye and Melville 1977), and the cycle of events was all but complete.

TOWARDS A RESOLUTION

In this review of the development of a stable scientific name for the chestnut teal, and the associated recognition of the grey teal as a distinct species, there is evidence of considerable confusion. Why was this so, why was there so much change, so much alteration to names applied by Eyton and Müller to what were accepted at times, in part or in whole, as valid species?

Initially there was confusion caused by the misapplication of Burchell's (1822) name *Anas punctata* to the Australian species. Gray (1844) considered, apparently, that this was a synonym of Eyton's (1838) castaneous widgeon *Mareca castanea*, and this assumption was followed by Gould (1845) and others. Since Burchell had described his widgeon as 'Entirely brown, excepting the chin, the cheeks, and a stripe from the eye, which are white' and Eyton had clearly detailed quite different plumages, particularly for the male, and gave his species origin as quite a different continent, the error is difficult to explain. Further, it appears that Cuvier had identified a specimen in the Paris Museum as *Anas punctata* and so labelled it (perhaps the source of his identification was Burchell 1822; certainly others listed this source in the annotated version of his work, Cuvier 1829); this manuscript appellation was then followed by Lesson (1831), Gray and subsequent authors without considering the original description or specimen, and with no regard for Cuvier's later reference. Perhaps too authors ignored, or were unaware of, often obscure literature and alterations may have been made in ignorance or without complete details. Certainly Newton (1871) drew attention to the use of Cuvier's name as an author, and commented on its dubious nature (see also Ride

et al. 1956); Meyer and Wigglesworth (1898) also dismissed Lesson's (1831) record of *punctata*. Subsequent events were, of course, to show that Burchell had been referring to a stiff-tailed duck (now *Oxyura maccoa*), that the Hottentot teal (now *A. hottentota*) had become involved in the confusion, and that there were in fact two Australian teal species, namely *Anas castanea* and *gibberifrons*, a prospect tentatively proposed by Gould, but ignored by many of the authors who followed him.

During the process of resolution, the use of various genera by different authors (e.g. *Mareca*, *Querquedula*, *Nettion* and *Nettion*) did little to clarify the situation but such generic names were applied at almost the whim of the designator, depending on what was considered to be the affinities of the species. Thus Eyton (1838), using *Mareca*, was suggesting that *castanea* was most closely related to widgeons, whilst placement within *Querquedula* (a genus subsequently in part replaced by *Nettion* and *Nettion*) implied garganey or teal-like attributes. Ultimately broader taxonomic grouping prevailed, and many such ducks were included within *Anas*, a genus within the sub family Anatinae — the true ducks. However, the creation of *Virago* by Newton (1871) and its acceptance and perpetuation by some authors (particularly Mathews) caused continuing confusion. In its erection, Newton considered that the species had unique features (i.e. the possession by the female of 'mas organa vocis'). The mistaken sex of the specimen was, however, adduced by later authors and the bullae ossea were not found in females subsequently dissected (e.g. Ramsay 1878c). Indeed, wrongly-sexed birds (not uncommon in other groups, e.g. in waders 'it is well known that some, and it can be over 25% in immatures, are incorrectly sexed', Prater *et al.* 1977) held in museums and other collections may have seriously influenced views on the status of *castanea* and *gibberifrons*, their distribution and, through disagreement on the dimorphic plumages, the acceptance of the existence of the species themselves. Certainly field observations were frequently in conflict with reports of those developing catalogues. Thus proposals that females had plumages resembling male *castanea* or that males might breed in essentially female plumage were to be dismissed by captive studies. Strangely though the myth continues: thus Serventy and Whittell (1976) in noting that 'as a rule' females lacked the vivid colours of the males, considered that 'On occasions females are found with the fully developed plumage of the male.'

The complete confusion of species led to considerable discussion on distribution. Propositions that *castanea* was found throughout Australia, New Zealand, New Caledonia and elsewhere were successively dismissed as it was realised that *gibberifrons* was a species in its own right, more widely distributed than *castanea*. In this review discussion of the New Zealand brown teal *A. aucklandica chlorotis*, and the Auckland Island teal *A. a. aucklandica*, have been ignored (but they too have had a complex series of nomenclatural changes and have, on occasion, been included within *castanea*, e.g. Fleming 1953). However, these birds, together with the earlier misidentification or misapplication of *gibberifrons*, may have been part of the source and reason for the inclusion of New Zealand in the range of *castanea*.

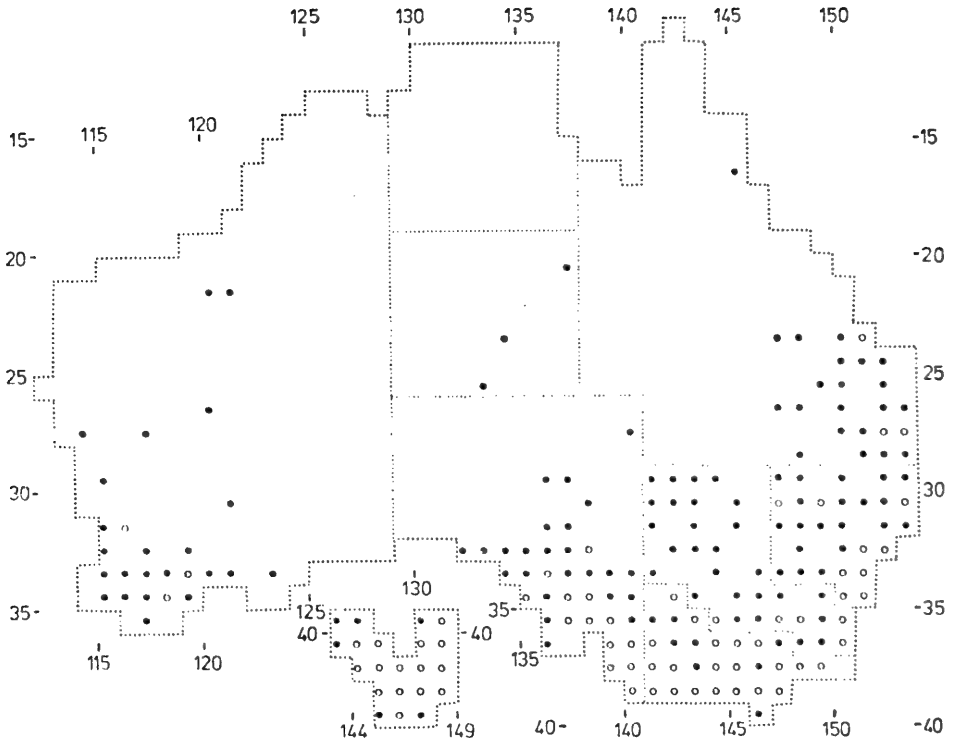


Fig. 1a

Fig. 1. Past and present distribution of *Anas castanea* (a) and *A. gibberifrons* (b) as determined from records held within the Royal Australasian Ornithologists' Atlas scheme. Open circles represent breeding records.

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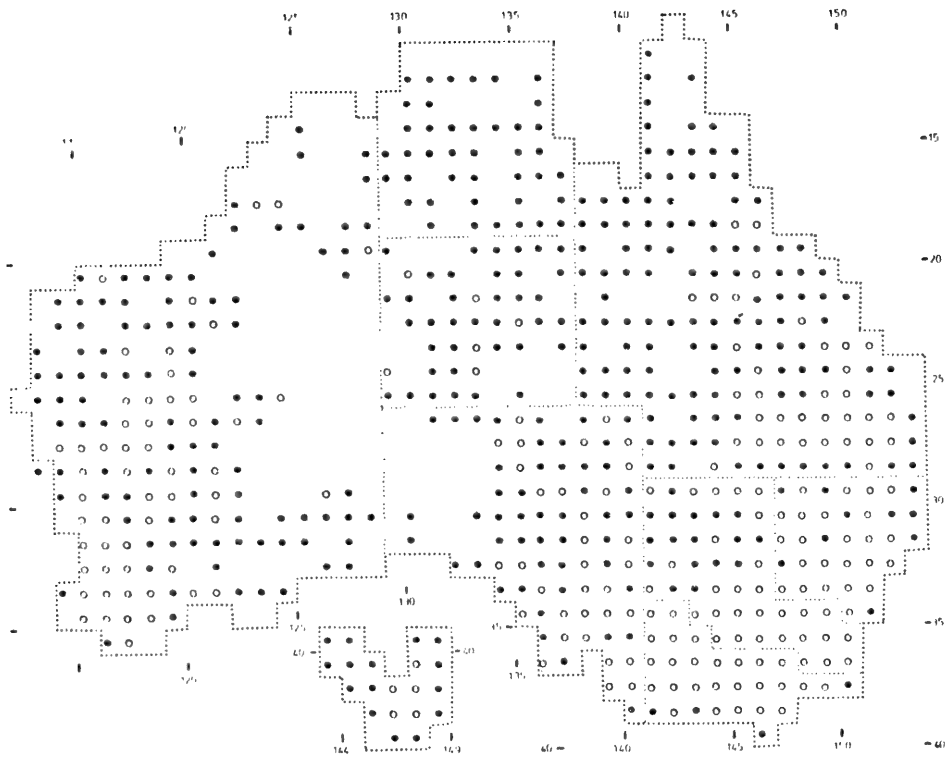


Fig. 1b

Thus Stidolph (1926) reviewed previous claims to the existence of *castanea* in New Zealand and concluded that he could find no valid record from 'the chaos created in the past'. All previous records were, Stidolph considered, referable to *gibberifrons*. Nevertheless, more recently Delacour (1965) recorded *A. aucklandica chlorotis* at Noumea. To add further confusion Stronoch (1980) reported a female chestnut teal from the Western Province of New Guinea: this was according to Stronoch a new species for New Guinea and others were subsequently reported (Stronoch 1981). Certainly within Australia the extensive series of field observations made by RAOU recorders support the view that *castanea* has generally a more southern and coastal distribution, whereas *gibberifrons* may be found throughout the continent (Fig. 1).

Earlier elucidation of the taxonomic confusion may also have been assisted by satisfactory investigation of aspects of the species' biology. There was, for example, an absence of a series of age characteristics (e.g. plumage and cloacal features), though the implication of the varying descriptions of iris colour (from the hazel of Gould 1845, to the red of Broinowski 1887 and others) might have been considered. Body parameters too were not discussed at length and specific size, for example, was not commented upon at all by earlier authors. Whilst Gould (1865) had noted that there were size differences within *punctata* (and raised the possibility of two species), other authors showed little interest in morphometric data. Though Salvadori (1880-1883) thought that the smaller birds, included in *punctata* by Gould, were in fact *gibberifrons*, of the authors reviewed above Keartland (1890a) appears to have been one of the earlier to present body weights in support of the contention that there were two species: he noted that male 'chestnut-breasted birds' were heavier, longer and had a greater wing span than the 'sombre Teal.' Increasingly such data were used by later authors to show that male and female *castanea* were substantially heavier than *gibberifrons* (e.g. Campbell 1901, North 1913). Indeed Campbell (1901) dismissed Salvadori's (1895) comment that the two females could not be distinguished easily from each other by pointing out that there was 'nearly a third difference in the weights.' However, Alexander (1916), in attempting clarification, merely added to the contemporary confusion by comparing a very small series of birds (including only two green-headed birds) with Keartland's information given in Mathews (1914-15). He found that all his sample was identifiable as grey teal, at least on a weight basis. Such misleading comparisons, based upon often trivial numbers of birds, also extended into other areas. Whilst Littler (1910), Mathews (1914-15) and North (1913), and Meyer and Wiglesworth (1898) before them, were amongst authors who gave various details of body, wing, tail, bill and tarsus lengths which showed, generally, the greater size of *castanea* compared with *gibberifrons*, Mathews suggested that individual variation related to differences in the sexes — at least in *gibberifrons*. Ramsay (1878b) also appeared to have dismissed size differences when examining two *castanea* and one *gibberifrons*, though he subsequently (Ramsay 1888) accepted both species.

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Confusion regarding plumage development and sexual plumage differences within *castanea* also affected the perception of species identification. This was confounded by a failure to appreciate that juvenal plumages may vary from those displayed by adults. Gould (1845) set the scene for later discussion when he reported that the adult male (of *punctata*) in winter adopted a female-like feathering, as also was worn by young. Though he later (Gould 1865) thought that there might be two species, separation of them using plumage characters was delayed with the varying inclusion of *gibberifrons* within the species 'complex'. This separation was certainly not assisted by the suggestion that both species could have a green-headed stage (e.g. Alexander 1916, Mathews 1914-15), one which perhaps varied with age or sex (Belcher 1914). Though it had been hinted at earlier, by authors such as Sclater (1882), it seems that it was only with Blaauw's (1916) more dogmatic refutation of this point that the matter achieved a degree of resolution. Not only did Blaauw show that the male's green head colour did not disappear, but he also noted that the young male *castanea* assumed an adult plumage when five to six months old. According to Blaauw, there was no eclipse plumage as such, but he accepted that there was some decrease in the intensity of colouration. Certainly Ripley's (1942) attempt to recombine *gibberifrons* with *castanea* was in part at least influenced by an imposition of an eclipse plumage onto the male *castanea*, and perhaps confused too by the inclusion of juvenal-plumage males (considered to be adults), or mis-sexed birds (see also Jones 1942). Whatever the reason for the retention of dimorphic plumages in *castanea*, and certainly it has presented considerable 'food for philosophical investigation' (Meyer and Wigglesworth 1898), it is not the consequence of an environmental stimulation of repressed genes as Ripley suggested.

The differing trinomials applied, usually with little apparent justification, played but a small role in the maturation process. They were, however, indicative of a more fundamental change which was to influence the taxonomy of all Australian birds and indeed the interest in taxonomy by all but few local workers. In the period reviewed here the concept of a species changed, from a discrete, static unit to a more dynamic system, and this was reflected in works of some authors. In this regard, a principal, dominant role was played by Mathews who, however, fluctuated between considering a species (and genus) as a small unit, to a ready acceptance of trinomials (and their implications), to narrow genera but broader species (see Serventy 1950). In addition, Mathews also showed a stubborn adherence to names established previously, frequently those which he had provided or unearthed. Thus he (Mathews 1946) was still advocating *Virago* long after other authors had discarded it, and he pursued the track of subspecies for some time (Mathews 1927).

Little of this controversy really troubled the amateurs or casual field workers. Contemporary observers, as distinct from the systematists, were happy to apply whatever specific name was considered appropriate at the time, and they were certainly not overly concerned with the process of taxonomic separation of the

species. Indeed there was often a use of a colloquial name alone, or one which might have a binomial appended. Thus Denham (1858) reported that he had obtained a 'Wild Duck' in Bass Strait, and termed it *A. punctata* (Cuvier); presumably the bird was a teal but indeed the record may be one of complete misapplication of a specific name. Others, such as Wheelwright (1865), well recognised the 'Australian teal'. Nevertheless, the gradual development of some accepted, and frequently used, common names is a reflection in part at least, of the changes in scientific opinion. Eyton's name, the castaneous widgeon, held little attraction, nor did spotted widgeon from Gray, but Gould's chestnut-breasted duck became a more popular epithet. Whilst Broinowski encompassed both species in using 'Australian teal', Keartland (1890a) noted that the chestnut-breasted teal was distinct from the common (grey) teal and reported that others (like Cotton years before) used 'mountain teal' for the chestnut species. And, towards the turn of the nineteenth century, there was an agreement that the chestnut-breasted teal (less frequently called mountain, Australian, black or even, by Mathews, eastern), was an appropriate common name to distinguish it from the grey (or slender) teal. Finally, the matter was officially resolved by the publication of the *Checklist* (RAOU 1926) in which the Ornithologists Union accepted the common names, chestnut and grey teal.

Eventually then, it was well accepted that there were two species, and that they were readily separable (*pace* Ripley). But the demolition of *punctata* from Africa and the final severing of its connections with *punctata* from Australia required a complex series of proposals for the deliberation of the International Commission in Zoological Nomenclature. In their review of previous usage of *punctata*, and the proposition that it should be validated for application to the Hottentot teal, Ride *et al.* (1956) indicated the confusion and complexity which had taken place. Their proposals were seen by some (e.g. Serventy 1956) as requiring the more liberal use of the Commission's powers, a change in their emphatic dependence on the Règles themselves. Dissension prevented voting at the time, but the matter was later revived in a revised form (Ride 1974). Whilst it was considered 'profondément *anti-historique* de supprimer un nom et absolument *anti-zoologique* de supprimer le nom d'un taxon dont le type existe' by one voter, the suppression of Burchell's *Anas punctata* was eventually achieved (Nye and Melville 1977). In this decision may also be seen the final resolution of the conflict between the binomials *gibberifrons* and *castanea*, the official endorsement of the rise of what was once called the castaneous widgeon *Mareca castanea*. But the problems of its historical distribution remain.

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A Survey of Fishways in Streams of Coastal South-eastern Australia

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ABSTRACT

A survey has identified 29 fishways on coastal streams of south-eastern Australia, between the Mary River in southern Queensland and Lakes Entrance in eastern Victoria. Only 9.2% of 293 dams and weirs and 23 causeways surveyed had provision for fish passage. Among 37 fish species native to the study area, about 70% require passage within river systems, either for survival or for maintenance of population abundance and distribution. Despite this need for fish passage, the behavioural responses and physiological limits of Australian fish that control their use of fishways are poorly known.

Of the 29 fishways recorded, 18 were of two metres or less in height, and none was higher than eight metres. Design, maintenance and water flow deficiencies resulted in 23 fishways failing to provide suitable conditions for fish passage at the time of the survey. Further biological research, more appropriate fishway design, and better supervision and maintenance of fishways are needed to conserve the region's fish fauna.

INTRODUCTION

Stream impoundment has been widespread in south-eastern Australia, but little attention has been paid to the needs of the fish fauna for passage past artificial barriers. However, many diadromous fish (which migrate between fresh-water and marine environments, usually to breed) are present, and their survival is not possible upstream of impassable physical barriers. Lesser barriers, are associated with a range of effects on stream ecology (Harris, in press).

Information relating to the few fish passage facilities built in Australia is sparse. Their construction and operation is the responsibility of many diverse authorities, and records of the incidence and characteristics of these structures are sketchy. Hooker (1966) has recorded the early history of fish passage in New South Wales. Beumer (1980) has referred to the existence in Australia of a total of about 53 fishways, and has reviewed the fish passage legislation in each of the states. Beumer and Harrington (1980) described a new fishway on the Lerderderg River in Victoria, and there have recently been fishway experiments conducted in Tasmania (Inland Fisheries Commission 1981). Eicher (1982) has discussed fish passage in New South Wales and the Australian Capital Territory.

Conference papers on the subject have reported many deficiencies of design and operation in fishways of south-eastern Australia (Harris 1980; Johnson 1981), and an unpublished report (Wilke and Johnson 1981) discussed some aspects of fishway design in Queensland.

The purpose of fishways is to channel water between different elevations so as to permit fish passage past obstacles. Fish movement is limited by velocity of flow, which is related to height and length of the fishway channel, and these factors largely determine the capital cost of the structure. Traditional fishway design has therefore involved a search for the means of most efficiently dissipating the energy of water flowing in steep channels. The considerable overseas literature on the many fishway types has been reviewed by Nemenyi (1941); Collins and Elling (1960); McGrath (1960); Trefethen (1968); Evans and Johnston (1974) and Brown (1980).

The overfall pool, submerged orifice, vertical slot and Denil types have become the most widely-used orthodox fishway designs (see Methods). The latter two are hydraulically very efficient, and have been used at slopes of up to 1 : 3 (Nemenyi 1941; Ziemer 1962; Slatick 1975). Newer devices which operate by trapping fish and actively transporting them in pipes, or in hoppers or buckets carried on trolleyways, cable systems or trucks, have also come to be classed as fishways.

Despite the fact that fishways have been constructed to designs developed originally for Northern Hemisphere anadromous species, the adaptability of Australian native species to these designs has not been reported upon, except for studies at Euston Weir on the Murray River by Langtry (Cadwallader 1977) and at the Fitzroy River Barrage (Kowarsky and Ross 1981). Morrissey (1980) considered that fishways were impracticable for barramundi, *Lates calcarifer*, but gave no evidence to support this statement. Fish passage through a new fishway at Casuarina Sands on the Murrumbidgee River is now being monitored (Department of the Capital Territory 1981).

A research program on the biology of the Australian bass, *Macquaria novemaculeata* included a study to quantify the artificial obstruction of migratory pathways throughout its range (Harris 1983a, and in press). Because of the need for effective fishways on dams and weirs to ensure survival of the bass and other diadromous fish, and to maintain the abundance and distribution of other species migrating in streams, a brief evaluation was made of the status of fish passage facilities in the coastal drainages of south-eastern Australia.

METHODS

The study area surveyed was defined by the range of Australian bass, that is, the coastal drainages of south-eastern Australia between the Mary River in southern Queensland and Lakes Entrance in eastern Victoria (Fig. 1). Site

FISHWAYS SURVEY

visits were carried out between December, 1978 and September, 1980. Sources of information have been defined elsewhere (Harris 1983a, and in press). The paucity of available information on the existence and location of fishways created considerable difficulties in finding sites. This fact, plus the size of the study area,

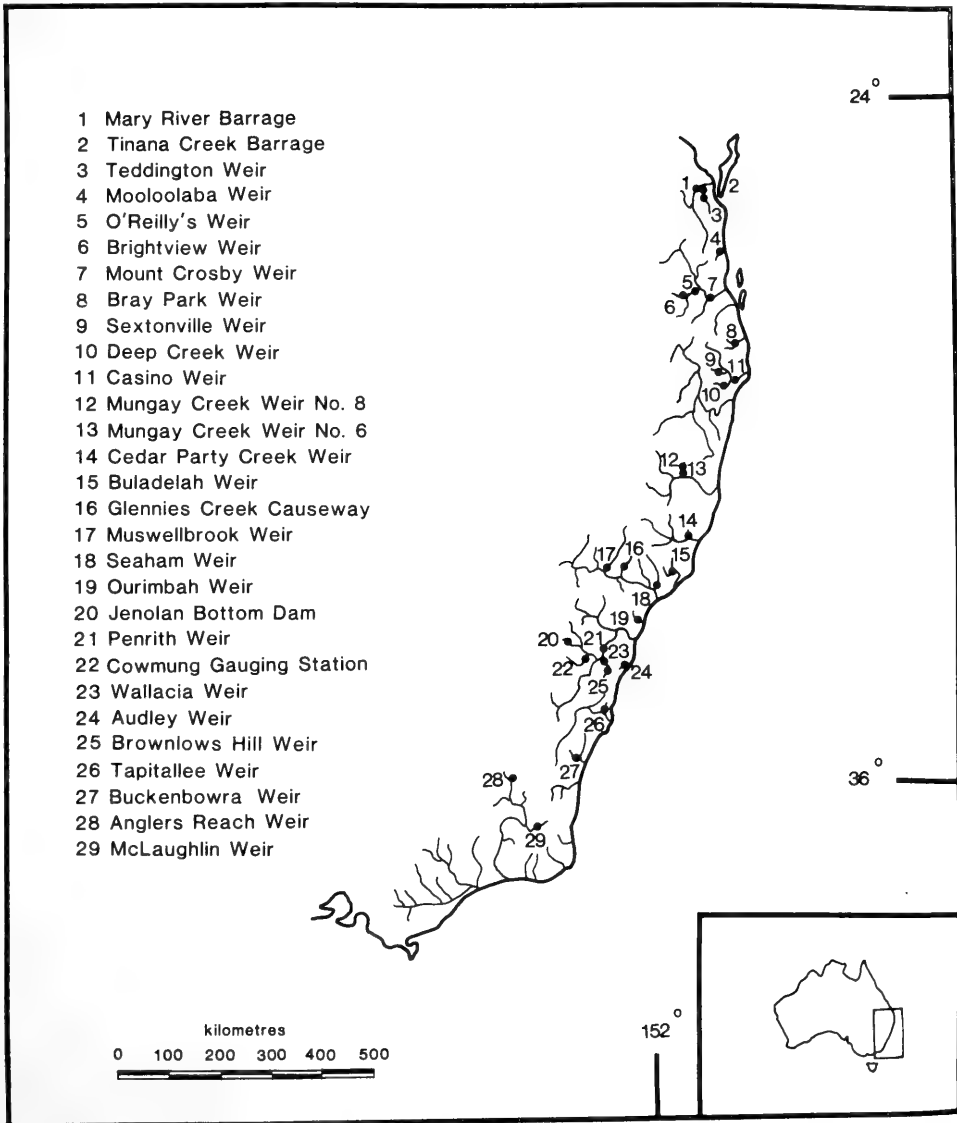


Fig. 1. Locations of fishways in streams of coastal south-eastern Australia.

and the commencement of two new structures restricted the number of sites that were visited to 19. Details of four other sites in Queensland were obtained from Queensland Water Resources Commission, and from a conference paper by Johnson (1981). Information on six other sites in New South Wales was obtained from the plans and site inspection records of the Water Resources Commission of New South Wales.

It was not possible to compare critically the functional efficiency of fishways because of the lack of flow and/or maintenance in most of them. However, a qualitative assessment of each structure was based on design features, location, water discharge and state of repair. Where possible, observations of water velocity were made at critical sections of fishways, using a simple flowmeter designed by Gessner (Hynes 1970). Although the generally poor condition of the fishways, and the variety of types represented, prevented the use of a standardised program of fish sampling, some structures were sampled by electrofishing, seining, trapping or dipnetting.

Fishway types were classified using the terminologies of McLeod and Nemenyi (1939); Committee on Fish Passes (1942) and Clay (1961) as follows:

- *Overfall pool* A fishway consisting of a series of pools separated by weirs, each about 15 to 45 cm lower than the preceding one. Water flows between pools by spilling over the crests of weirs.
- *Submerged orifice* A pool-type fishway in which water flows between pools through an orifice located in the base of each weir.
- *Overfall pool and orifice* This pattern combines the features of 1 and 2.
- *Vertical slot* A fishway in which the pools communicate through a vertical slot in each weir.
- *Denil type* This pattern utilises a series of closely spaced baffles on the sides of the fishway to impede the velocity of flow without causing excessive turbulence.

RESULTS

INCIDENCE OF FISHWAYS

A list of 29 fishways was compiled, seven of which were in Queensland and the remainder in New South Wales. Table 1 lists the height, type and other details for each structure, and Figure 1 maps their locations. The fish migration barriers surveyed included 293 dams and weirs (Harris in press). A sample of 23 of the road crossings that impede fish movement within the study area was also listed, and one of these, the Glennies Creek causeway, incorporated a simple fishway. Thus the overall frequency of occurrence of fishways on these artificial barriers was 9.2%.

Figure 2 illustrates the frequency distribution of fishways related to the height of barriers. Fishways were only incorporated in the smaller structures. The highest

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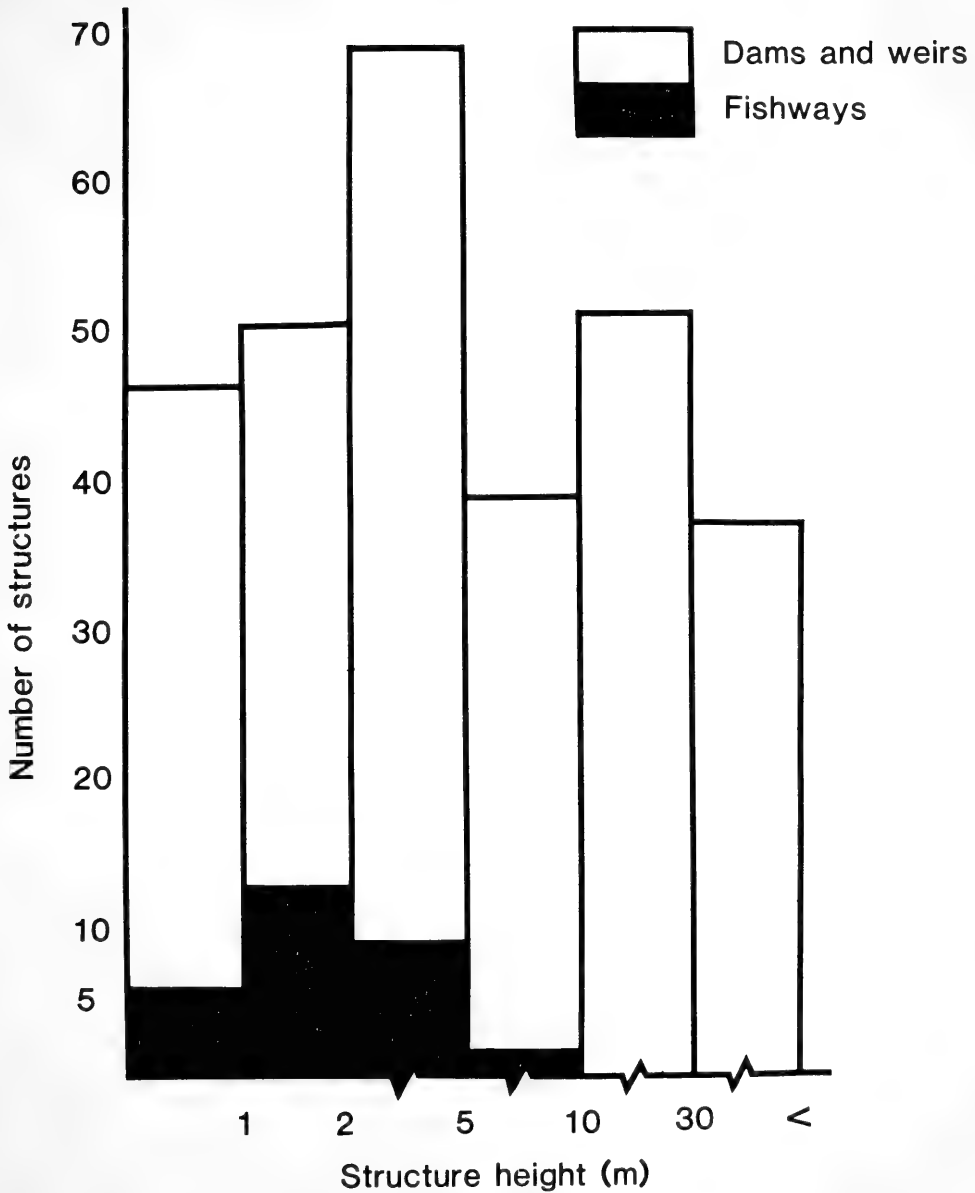


Fig. 2. Occurrence of fishways on dams and weirs in the study area, related to the heights of these barriers.

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Fishway No.	Barrier	Stream	Nearest town	Type	Ht.	Flow control	Comments
1	Mary River Barrage	Mary R.	Maryborough	2	3	Stop board	Under construction *
2	Tinana Creek Barrage	Tinana Ck.	Maryborough	2	3	?	Under construction *
3	Teddington Weir	Tinana Ck.	Maryborough	3	6	Sluice valve	Fishway dry, valve shut. Separate outlet sluice. Entry distant from spillway.
4	Mooloolaba Weir	Mooloolo R.	Mooloolaba	2	1.6	Sluice valve	Fishway dry, valve shut.
5	O'Reilly's Weir	Lockyer Ck.	Gatton	3	5.2	None	Poor hydraulic performance. Entry distant from spillway. Separate outlet sluice.
6	Brightview Weir	Lockyer Ck.	Lowood	1	8	None	Entry distant from spillway. Separate outlet sluice.
7	Mount Crosby Weir	Brisbane R.	Ipswich	1	3	None	No flow. Spillway discharges minor flows. Entry distant from spillway.
8	Bray Park Weir	Tweed R.	Murwillumbah	2	1	Sluice valve	No flow. Valve shut.
9	Sextonville Weir	Richmond R.	Casino	2	4	Stop board	Orifices blocked.
10	Deep Creek Weir	Doubtful Ck.	Kyogle	2	2	Sluice valve	Fishway dry, valve shut.
11	Casino Weir	Deep Ck.	Casino	2	2	Sluice valve	Fishway dry, valve shut.
12	Mungay Creek Weir No. 8	Mungay Ck.	Kempsey	1	2	None	Fishway dry. Spillway at same level as fishway intake.
13	Mungay Creek Weir No. 6	Mungay Ck.	Kempsey	2	1.5	Stop board	Fishway normally shut off.
14	Cedar Party Creek Weir	Cedar Party Creek	Wingham	2	2	Stop board	Fishway normally shut off.
15	Buladelah Weir	Crawford R.	Buladelah	2	0.6	Sluice valve	Fishway dry, valve shut.**
16	Glennies Creek Causeway	Glennies Ck.	Muswellbrook	5	0.6	None	Fishway dry. Poor design.
17	Muswellbrook Weir	Hunter R.	Muswellbrook	?	1	?	Destroyed by floods.
18	Seaham Weir	Williams R.	Seaham	4	1.5	Stop board	Functioning. Entry distant from spillway flows. Partly blocked.
19	Ourimbah Weir	Ourimbah Ck.	Ourimbah	2	2.7	Flap valve	Fishway dry, valve shut. Narrow exit pipe upstream.
20	Jenolan Bottom Dam	Jenolan R.	Oberon	1	3	None	Top weir 45 cm high. Partly blocked. Entry distant from spillway.

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Fishway No.	Barrier	Stream	Nearest town	Type	Ht.	Flow control	Comments
21	Penrith Weir	Nepean R.	Penrith	1	1.6	None	Entry distant from spillway. Spillway at same level as fishway intake. Blocked.
22	Cowmung Gauging Station	Cowmung R.	Oakdale	1	0.5	None	Functioning.
23	Wallacia Weir	Nepean R.	Wallacia	1	3.3	None	Fishway dry. Spillway at same level as fishway intake. Entry distant from spillway.
24	Audley Weir	Hacking R.	Sutherland	?	1.8	?	Fishway destroyed by roadwork.
25	Brownlows Hill Weir	Nepean R.	Camden	1	3.9	Sluice valve	Fishway dry, valve shut. Poor entry. Fishway blocked.
26	Tapitallee Weir	Tapitallee Creek	Nowra	2	1.3	Sluice valve	Fishway dry, valve shut.
27	Buckenbowra Weir	Buckenbowra River	Batemans Bay	2	0.6	Sluice valve	No flow. Valve shut. Spillway at same level as fishway entry.
28	Anglers Reach Weir	Long Plain Creek	Adaminaby	1	1.4	None	Damaged by floods. Partly blocked.
29	McLaughlin Weir	McLaughlin River	Nimmitabel	1	1.5	None	Functioning.

TABLE 1. Details of fishways on coastal streams in south-eastern Australia, 1978-1980. Fishway types, with the total number of each in brackets are: 1. Overfall pool (10). 2. Submerged orifice (13). 3. Overfall pool and orifice (2). 4. Vertical slot (1). 5. Denil type (1). Unknown (2). "Ht." indicates height of barrier (m).

* Mary River Barrage and Tinana Creek Barrage fishways have vertically elongated submerged orifices.

** Buladelah Weir fishway was flowing when revisited on 2.12.1981.

fishway (at Brightview Weir) was only eight metres high, and 18 of the remainder were of two metres or less in height. Fishways were incorporated more frequently into structures which obstructed the smaller streams. Only nine of the total of 29 structures served the fish populations of larger rivers.

There was one Denil type and one vertical slot type fishway; two overfall/orifice types; and ten overfall pool type. The submerged orifice type was the most frequent (13), including the unfinished Tinana Creek Barrage and Mary River Barrage fishways that are intermediate between the submerged orifice and vertical slot types. The design of the two destroyed fishways at Audley Weir and Musswellbrook Weir is unknown.

EFFICIENCY OF FUNCTION

Two fishways, at Cowmung Gauging Station and McLaughlin Weir, were considered to provide suitable conditions for passage of local fish populations (principally trout). Mary River Barrage and Tinana Creek Barrage were still under

construction, and insufficient information was available to make an assessment of Brightview Weir fishway. The status of Seaham Weir fishway is uncertain because of its susceptibility to blockage and the lack of knowledge of the behaviour and swimming capacity of juvenile catadromous fish (that is, diadromous species migrating from freshwater to spawn in a marine environment) at tidal barriers.

For the various reasons annotated in Table 1, the remaining 23 fishways produced conditions that were considered unsuitable for the passage of the local migratory fish. It was considered, however, that many of these could be made to provide some fish passage under favourable stream flow conditions by removal of flow controls, by routine maintenance, and, in some cases, by minor modifications.

Eight of the fishways were found to have the downstream entry distant from the spillway, a fault which often causes fishway failure (Clay 1961). A lack of maintenance was found to prevent or limit the function of eight fishways. The structure at Muswellbrook Weir had been destroyed by floods, and the Anglers Reach fishway had been similarly damaged. Fishways at Penrith Weir, Seaham Weir, Brownlows Hill Weir, Jenolan Bottom Dam, Anglers Reach Weir and Casino Weir were affected by accumulations of stream bed substrate and debris, which obstructed the flow to varying degrees. The fishway at Audley Weir was destroyed during road reconstruction in 1955, but not replaced. Johnson (1981) reported violent surging in the water flow through O'Reilly's Weir fishway.

CONTROL OF FLOW

Means of controlling flow were provided on 15 of the fishways, in the form of sluice valves or stop boards. Of these structures, 12 either had no water flowing through them when visited, or are normally kept dry (Table 1). Of the 11 fishways that did not have flow control devices, five carried only a minor proportion of stream flow because the dams and weirs on which they were built had large separate spillways at about the same intake level (Mount Crosby Weir, Mungay Creek Weir No. 6, Glennies Creek causeway, Penrith Weir, Wallacia Weir). These fishways may function at periods of high stream discharge, but carry little or no water during times of lesser flow.

WATER VELOCITIES AND FISH OBSERVED

Peak water velocities over the weirs of Mount Crosby Weir fishway averaged 220 cm/s. Small numbers of sea mullet, *Mugil cephalus* (7 to 15 cm in length), and rainbowfish, *Nematocentris fluvialis*, as well as shrimp, *Macrobrachium* sp. were observed moving through the fishway. At Buladelah Weir fishway water in the intake pipe, of several metres length, was flowing at an average velocity of 130 cm/s. No fish were seen to pass through the pipe.

Many fish were found in the lower two cells of Seaham Weir fishway, including eels, *Anguilla reinhardtii*; bullrout, *Notesthes robusta*; sand mullet, *Myxus elongatus*; yellow perchlet, *Priopodichthys marianus*; sea mullet; and one

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juvenile Australian bass. It was not possible to determine what fish species successfully negotiated the Seaham Weir fishway. Fourteen juvenile Australian bass were found in the lower end of Penrith Weir fishway, beneath an overfall weir of greater than average height, but none was found above this point in the fishway. Many Cox's gudgeons, *Gobiomorphus coxii*, negotiated the fishway by climbing the wet sides of each pool.

Between one and three rainbow trout, *Salmo gairdnerii*, of 9 to 16 cm length were taken in each pool of the Jenolan Bottom Dam fishway. These fish may have been resident in the pools. Mean peak water velocity over the bottom weir was 154 cm/s. Cowmung Gauging Station fishway was flowing at a mean peak velocity of 170 cm/s. No fish were observed, but Water Board Rangers reported that large spawning runs of trout pass through the fishway.

At all the fishways except Cowmung Gauging Station, there were large accumulations of fish below the fishway entry. This suggested that a substantial proportion of the fish were obstructed while seeking upstream passage.

Species	Common name	Migration
<i>Anguilla australis</i>	Short-finned eel	C
<i>A. reinhardtii</i>	Long-finned eel	C
<i>Galaxias maculatus</i>	Common jollytail	C
<i>Geotria australis</i>	Pouched lamprey	A
<i>Lates calcarifer</i>	Barramundi	C
<i>Macquaria novemaculeata</i>	Australian bass	C
<i>Mordacia mordax</i>	Short-headed lamprey	A
<i>M. praecox</i>	Non-parasitic lamprey	A
<i>Myxus petardi</i>	Freshwater mullet	C

TABLE 2. Fish species of the study area known to have an obligatory migratory stage in their life cycle. "A" indicates anadromous species, "C" catadromous. Many other species are believed to be migratory (see text).

DISCUSSION

Migratory patterns of Australian freshwater fishes are poorly documented, and the ecological significance of obstructing fish passage through Australian drainage systems has seldom been examined. However, information on the subject is reviewed in another paper (Harris, in press), and Table 2 lists the fish species of the study area presently known to have an obligatory migratory stage in their life cycle. In addition to these nine fishes, there are many other species whose life cycle is probably potamodromous (that is, they migrate within river systems), or diadromous. Of about 64 species found in freshwater in the study area, 17 have been introduced from overseas or other drainages in Australia, and 10 are essentially marine species that may spend some time in freshwater. Twenty-six of the remaining 37 species (70%) appear to be migratory, although this is not obligatory in five cases. Six migratory species (young eels, lampreys, and the climb-

ing galaxias, *Galaxias brevipinnis*) are able to climb wet vertical surfaces, and do not always require the provision of fishways.

Dams, weirs and tidal barriers affect fish populations in one half of the habitat potentially available in the coastal drainages of south-eastern Australia (Harris, in press), but only 9.2% of these artificial barriers to migration included any provision for fish passage. Apart from Brightview Weir, no attempt has been made to provide fishways on the 100 dams of eight metres height or more. The greater capital cost of tall fishways, the lack of design criteria tested in Australian conditions, and the generally low level of study of the natural history, behaviour and physiology of the fauna have all contributed to these deficiencies.

TIDAL FISHWAYS

Among the 30 tidal barriers in the study area, the only sites at which an attempt has been made to provide fish passage, and overcome the difficulties caused by tidal movement that were found by Brawn (1979) and Kowarsky and Ross (1981), are Seaham Weir, Mary River Barrage and Tinana Creek Barrage. At least six, and probably eight catadromous species inhabit the study area (Table 2). Tidal barriers can have a major impact upon the upstream abundance of such catadromous fish (Harris 1983b), because of the small body size and very limited swimming ability of their upstream-migrating larvae and juveniles.

Thus fishways on tidal barriers need to meet very conservative water velocity criteria. Few data are yet available to establish these criteria for south-eastern Australian conditions, but Delta Fish And Wildlife Protection Study (1967) studied the performance of juveniles of several salmonid, centrarchid and percid fishes in a vertical slot fishway, and recommended that average water velocities not exceed 45 cm/s to 60 cm/s. Wilke and Johnson (1981) concluded that young sea mullet, 30 to 50mm long could reach a burst swimming speed of 145 cm/s for up to two seconds. Kerr (1953) found that young striped bass, *Morone saxatilis* 25mm long were unable to withstand a velocity of 43 cm/s for 10 minutes, but were able to swim against a flow of 30 cm/s for 10 minutes. This speed approximates 10 body lengths per second, which was the general rule derived by Bainbridge (1958) to indicate the likely maximum sustained (for one minute) swimming speed of fishes.

Total lengths of juvenile Australian bass migrating upstream from estuaries have been found to be between about 29 mm and 35 mm (Harris 1983b), so that a mean water velocity of about 30 cm/s would appear to be a reasonable starting point for flow-rate trials in experimental tidal fishways. Less stringent criteria are needed for fishways located in the headwaters of stream systems because of the greater age, body size and locomotor ability of catadromous fishes (such as young Australian bass, which migrate upstream over a period of six to eight months) using these structures.

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FISHWAY TYPES

Within the study area the submerged orifice type of fishway has been the most frequently used (13), followed by the overfall pool type (10). However, many studies have shown that these fishways are less able to function under a wide range of flow conditions than are the vertical slot and Denil types (McLeod and Nemenyi 1939; Committee On Fish Passes 1942; Clay 1961; Eicher 1982). Clay (1961) reported higher peak water velocities in the submerged orifice fishway than in other common types. Eicher (1982) also considered the vertical slot and Denil fishways to be more economical of water. Wilke and Johnson (1981) found that young sea mullet could negotiate fishway pools with a greater pressure head between them if the pools were connected by a slot rather than an orifice.

Obstruction by bed load (large substrate particles) was found at five fishways within the study area. This is a problem that, as well as being related to the location and height of the barrier, is less likely to affect vertical slot and some types of Denil fishways, because of their greater self-scouring ability (Clay 1961; Ziemer 1962). Eicher (1982) considered that the vertical slot and the Maine version of the Denil fishway held the most promise for the passage of native fish past weirs and low dams in New South Wales. This opinion is supported by the observations of Fulton *et al.* (1953); Fisk (1959); Ziemer (1962); Bell (1975) and Slatick (1975). Seaham Weir on the Williams River was the only vertical slot fishway found in the study area. Plans for the Mary River Barrage and Tinana Creek Barrage fishways utilize some of the features of the vertical slot type. The Glennies Creek causeway had a fishway that appeared to copy some of the Denil principles, but was of unusual design.

FISHWAY ENTRANCES

The behavioural responses and physiological limits of Australian fish that control their use of fishways are virtually unknown, except for the observations on sea mullet by Kowarsky and Ross (1981) and Wilke and Johnson (1981). However, the fishway entrance has been considered by most authors to be the critical design area. Most cases of poor fish usage of fishways are caused by failure of the entrance to stimulate appropriate behaviour in migrating fish. The entrance must be sited as far upstream as possible. It must also have a sufficient discharge to be detectable by fish, and must be directed so as to lead them to the entrance (McGrath 1960; Clay 1961; Bell 1975; Eicher 1982). Delta Fish and Wildlife Protection Study (1967) and Dominy (1973) also found that depth was an important characteristic of the entrance.

Collins (1952); Collins and Elling (1960) and Weaver (1963) have noted the importance of water velocity at fishway entrances, the response of fish varying according to species. Clay (1961); Trefethen (1968); Eicher (1973) and Bell (1975) discuss the use of controlled discharge from the spillways of dams and weirs in leading migrant fish towards the fishway entrance, and of auxiliary flows

to attract them into the structure. These various principles of fishway entrance design were rarely, if ever, observed in the fishways of the study area.

Structures with a well-located entrance, and which discharged water in a manner considered likely to be readily detectable by fish, were Buladelah Weir, Cowmung Gauging Station, Anglers Reach Weir and Maclaughlin Weir. Entry location is less of a problem in little streams because of the smaller search area that must be covered, and because a greater proportion of the total flow can be carried by the fishway channel, thus providing a more prominent orientational cue. Plans for the Mary River Barrage provide for a fishway entry at the face of the barrage, and the lowering of the adjacent spillway crest to concentrate the flow in this area, which should aid fish orientation. Nine other structures (Mooloolaba Weir, Bray Park Weir, Sextonville Weir, Deep Creek Weir, Mungay Creek Weir No. 8, Cedar Party Creek Weir, Seaham Weir, Ourimbah Weir and Buckenbowra Weir) could be modified so as to achieve reasonable fishway entrance conditions.

WATER FLOW

Drought conditions existed throughout the study area during the survey, causing a general reduction in stream flows. However, each of the fishways that was recorded as carrying minimal or nil flows (Table 1) either had flow control devices fitted, or was built upon an impoundment having a large separate spillway at the same or lower fixed crest level. Of the 23 fishways on which sufficient information was obtained, 18 were considered to carry less than the discharge that was potentially available for fish passage. It was therefore concluded that the drought had not biased the results of these observations, but merely made the problem of inadequate flow more readily apparent. It is likely that fishways have been designed with these flow-control features so as to retain the greatest possible amount of stored water in the impoundments.

This illustrates a fundamental conflict of interest which can arise in the provision of fish passage. Fluctuating stream flow regimes characterise Australian drainage systems, because of seasonally variable and unreliable rainfall patterns, and the frequent occurrence of droughts. Thus the difficulties created by demands for water conservation are compounded by the need for Australian fishways to function for much of the time in conditions of low stream flow, when some fish species may migrate (Harris, *in press*).

However, fishway designs exist that effectively utilise most of an impoundment's discharge for fish passage, over a large portion of the flow duration curve, without excessive usage of water (Clay 1961; Eicher 1982). Moreover, seasonal patterns of migration in various species may determine the needs for fishway function and water usage at particular times. For example, juvenile bass migrants probably require passage during only a few months, between November and May, and for only a few hours each day (Harris 1983b).

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There are also less traditional types of fish passage facilities that do not compromise the need to conserve stored water, and that suit high dams. These include trap and haul systems (Norris *et al.* 1960; Layzer 1979), cable and trolley-way transportation (Clay 1961; Eicher 1964), fish locks (Anon. 1950; Murphy and Dooge 1951), and pumped transport (Kerr 1953; Eicher 1964, 1982). Sloane (1981) reported the successful use of a pump to lift elvers past the Trevallyn Power Station in Tasmania.

CONCLUSION

Current standards of maintenance and control of fishways in the study area are plainly inadequate, and a very small proportion of the few existing fish passage facilities are effectively serving their purpose. The welfare of many native fish species, some of which are of substantial commercial or recreational importance, is threatened. There is a clear need for a far more frequent provision of fishways at artificial barriers in the coastal drainages of south-eastern Australia, and for substantial improvements in their design. Basic design criteria and technology are already available to enable experimental fish passage studies at large dams and smaller barriers. These fishway designs must now be adapted to suit local conditions, and behavioural research is urgently needed to test the responses of Australian fish to them.

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Impoundment of coastal drainages of south-eastern Australia, and a review of its relevance to fish migrations

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ABSTRACT

A study was carried out to estimate the proportion of the freshwater fish habitat in coastal drainages of south-eastern Australia that has been affected by stream impoundments. Two separate methods were applied, each using the results of a survey of stream impoundments and 1:1,000,000 maps. The methods used estimated the proportions of, first, the total stream length that had been obstructed, and second, the total number of streams that had been obstructed. The results indicated that fish passage in about half of the aquatic habitat of Australia's south-eastern coastal drainages has been obstructed by dams, weirs and other man-made physical barriers.

Migratory patterns of the region's fish species were reviewed. Ways in which impoundments affect the 26 species that were identified as migratory are discussed in relation to the ability of fish to bypass barriers, the nature of their migrations, and the role of flooding. The presence of about eight catadromous species in the region creates a special problem in fish passage. It is concluded that there is cause for concern over the status of the region's fish populations, and that there is a need for a much greater awareness of the nature and extent of this problem.

INTRODUCTION

Native fishes of streams draining the coastal region of south-eastern Australia have received little study, and their biology remains poorly understood (Williams 1973; McDowall 1981). However, many of the species undergo some form of migration, and widespread impoundment of streams with dams, weirs and other physical barriers has led to concern over possible effects on the abundance and distribution of these fishes (Lake 1971; Bishop and Bell 1978; Bishop and Tilzey 1978; Bell *et al.* 1980). Impoundment of waterways has affected the fish fauna of the Murray-Darling River system by obstructing fish passage and by suppressing breeding (Lake 1967a; Cadwallader 1978; Walker 1979). Man-made physical barriers have often diminished the spawning runs of anadromous fish in Northern Hemisphere rivers (Davidson *et al.* 1943; Elder 1965; Fraser 1972a, 1972b).

Because control over the construction of physical barriers in Australian streams is fragmented, and only limited records are kept, there is a lack of information on their occurrence and features. However, data on the major impoundment works

of the south-eastern coastal region are provided by Aird (1961); W.C.I.C. (1971); Munro (1974); A.W.R.C. (1976); A.N.C.O.L.D. (1976); and I.C.S.D. (1978).

Details of smaller physical barriers within the region such as weirs, private farm dams, road crossings and flood control devices are very poorly documented. The effects of these smaller barriers upon the fish fauna have seldom been discussed, except for references to Murray River weirs (Reynolds 1976; Walker 1979), Tasmanian data (Sloane 1979), and a report on fish passage in New South Wales (Eicher 1982).

This paper analyses the impoundment of coastal streams in south-eastern Australia, and estimates the resulting loss of habitat. A review of the migratory patterns of the fish fauna is combined with an examination of the effects that different types of man-made physical barriers may have on fish.

METHODS

INCIDENCE OF OBSTRUCTION

The analysis of stream impoundment was based on data from a census of man-made physical barriers in the geographic range of Australian bass, *Macquaria novemaculeata* (Harris 1983a) (Fig. 1). The range includes eastern-flowing drainages from the Mary River in Queensland to Lakes Entrance in Victoria (Fig. 1) (Williams 1967; Harris 1983b). This study area was divided into 22 drainages, based on major river systems or appropriate arbitrary divisions. Impoundments were allocated to one of the following four categories, depending on the drop in water level, and whether they formed the limit of tidal penetration:

Weirs: Impoundments less than 3 metres high.

High Weirs: Impoundments with a height of 3 to 7 metres.

Dams: Impoundments having a height exceeding 7 metres.

Tidal Barriers: Impoundments of any height that form the limit of tidal penetration in a stream.

In census field work, impoundment height was simply measured as the difference between upstream and downstream water levels. However, heights for many impoundments were obtained from published data, which are usually expressed as the total height of the dam wall, including foundations. Published dam heights were therefore corrected by using a formula derived empirically from several examples:

$$He = 0.85 (Ht - 1)$$

where "He" is the effective impoundment height in metres, and "Ht" is the total wall height as listed. This formula gave a reasonable approximation of the drop in water level, enabling impoundments to be allocated to the appropriate category.

IMPOUNDMENTS AND FISH MIGRATION

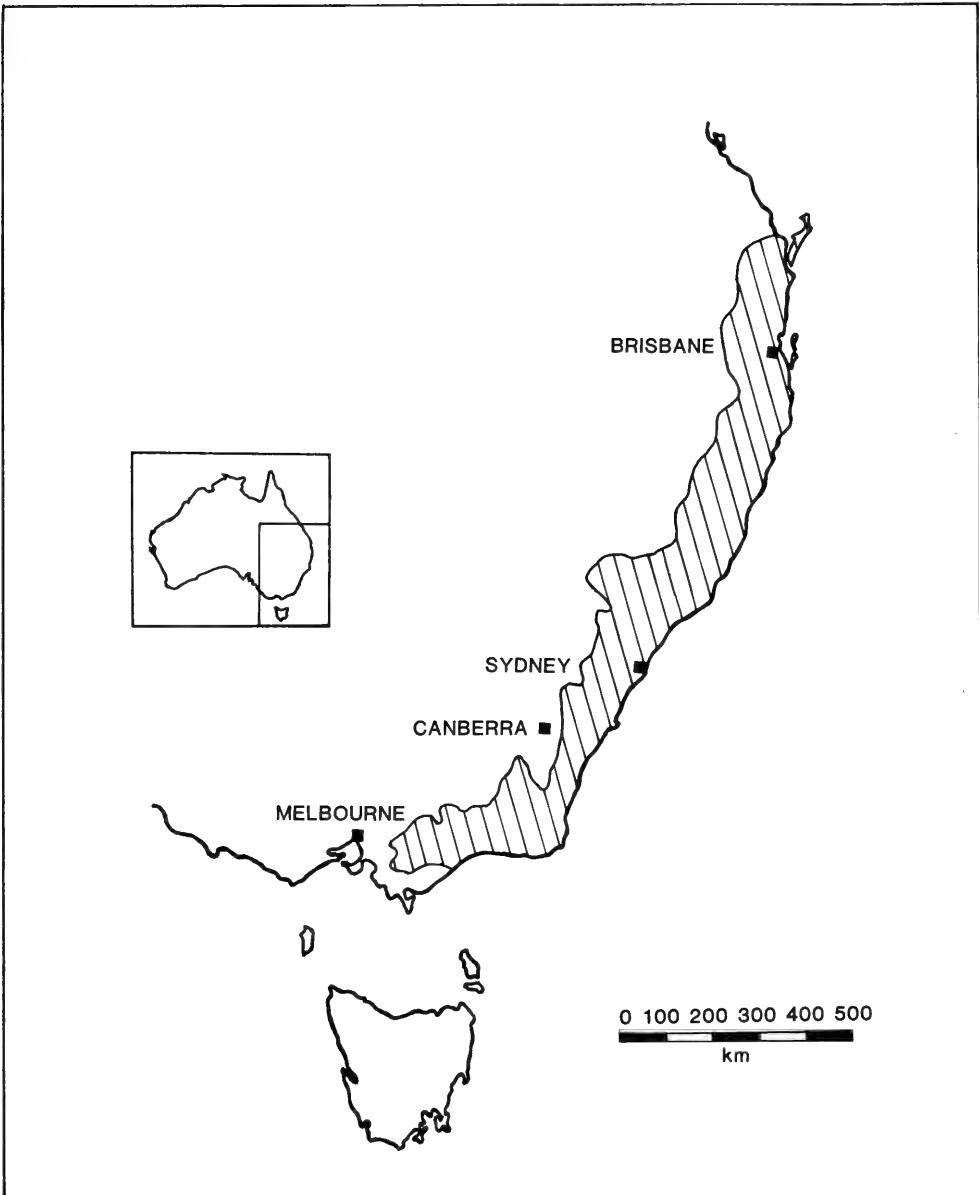


Fig. 1. Drainage systems within the geographic range of Australian bass, *Macquaria novemaculeata* (diagonal hatching).

Tidal barriers were considered, together with dams, as "major barriers" because they obstruct larvae or small juveniles of catadromous species (see later) in their upstream migration. To such fish in tidal habitats, these structures can present an insurmountable obstruction.

PROPORTION OF FISH HABITAT OBSTRUCTED

Two separate methods were used to estimate the proportion of the total habitat in which fish populations were affected by the obstruction of free passage caused by man-made physical barriers. Each method was based on the census of impoundments (Harris 1983a) and on the 1:1,000,000 International Map of the World Series of the Australian Division of National Mapping. This series was chosen for ease of measurement and because intermittently flowing or ephemeral streams are not recorded.

METHOD 1: PROPORTION OF TOTAL STREAM LENGTH THAT IS OBSTRUCTED

A simplified form of measurement, the "smoothed valley length", was devised to measure total stream length in each drainage system. "Obstructed" smoothed valley lengths were then recorded as the total distance upstream of impoundments.

Smoothed valley length data were logged with a Hewlett-Packard micro-computer and digitiser, using a graphics board and cursor to log curvilinear distances. The "smoothed" length of each stream was logged by tracing the general course of its valley with the cursor. Minor stream sinuosities and curvatures were ignored. This valley smoothing technique gives no indication of the absolute dimensions of the available aquatic habitat, but it has been used to estimate the proportion of habitat obstructed.

The small scale of the maps used tends to shorten the real length of streams by excluding smaller tributaries in the headwaters. Because this occurs upstream of impoundments, the smoothed valley length method gives a conservative estimate of the proportion of the habitat obstructed.

METHOD 2: PROPORTION OF THE TOTAL NUMBER OF STREAMS THAT ARE OBSTRUCTED

Streams named on maps as "rivers" were assumed to be an unbiased sample of the waterways of the region. A river was recorded as "obstructed" if one or more of the four classes of physical barrier were present:

- In its main channel
- Downstream of its junction with a confluent river into which it drained,
or
- In any of its tributaries.

IMPOUNDMENTS AND FISH MIGRATION

By ignoring the segment of each obstructed stream that is downstream of the physical barrier, this technique tends to overestimate the obstructed proportion of the total habitat. However, although dams occur more frequently in the upper parts of drainage systems, tidal barriers are free of this bias. No particular pattern is apparent in the distribution of the weirs and high weirs along streams.

Four types of man-made physical barriers were excluded from the census. They were road crossings, farm dams, flood control works, and structures (such as off-stream pumped storage dams or road crossings with piped stream flow) that were not considered to obstruct the passage of aquatic animals. Natural barriers such as waterfalls were not recorded.

NUMBER OF MIGRATORY FISH SPECIES

Native fishes of the area were classified according to their migratory patterns. Because of the paucity of information on the biology of most of these species, the terminology of Myers (1949) was adapted as follows:

"Diadromous": Migratory fishes which regularly migrate between the sea and freshwater, usually to breed.

"Anadromous": Diadromous fishes which spend most of their lives in the sea and migrate to freshwater to breed.

"Catadromous": Diadromous fishes which spend most of their lives in freshwater and migrate to the sea to breed.

"Amphidromous": Diadromous fishes whose migration from freshwater to the sea, or *vice versa*, is not for the purpose of breeding, but occurs commonly in a substantial proportion of the population.

"Potamodromous": Truly migratory fishes whose migrations occur wholly within freshwater.

McDowall (1968) pointed out that Northern Hemisphere literature had often incorrectly applied this terminology to Australasian fish.

RESULTS

A total of 293 physical barriers were listed in the census, including 111 dams, 30 tidal barriers, 96 weirs and 56 high weirs. Physical barriers were recorded in all drainage systems, although highly-developed areas had the greatest incidence of stream impoundment. The seven most settled areas of the 22 drainages (Brisbane, Gold Coast, Hunter, Hawkesbury, Sydney, Illawarra and Lakes Entrance) together contributed 70% of the total number of dams in the study area.

The Hawkesbury River system near Sydney was the most extensively modified, with 80 impoundments, of which 32 were major barriers. The Clyde, Hastings and Manning River systems in New South Wales had the lowest incidence, with two structures in each. The occurrence of physical barriers in the 22 drainages is summarised in Table 1, together with the presence of flood control schemes in drainages, in which each scheme uses a variable number of separate structures. Table 2 classifies these impoundments according to their primary purpose.

TABLE 1. Occurrence of impoundments in the study area, and the proportions of drainage systems lying upstream of these physical barriers.

DRAINAGE SYSTEM	CLASS OF IMPOUNDMENT*					SMOOTHED VALLEY LENGTH (km)				
	Total	Weirs	High Weirs	Dams	Tidal barriers	F.C. Schemes	Total	Above† major barriers	% of total barriers	% of total barriers
Mary River	5		1	2	2		1,028	978	95	978
Queensland South Coast	6	1		5			397	64	16	77
Brisbane River	14	2	2	9	1	+	1,433	1,288	90	1,288
Gold Coast	8			7	1	+	991	221	22	221
Richmond River	23	17	1	4	1	+	1,182	70	6	169
Clarence River	7	3	1		3	+	4,620	12	0	495
N.S.W. North Coast	5	1		1	3	+	1,091	65	6	270
Macleay River	12	5	2	5		+	2,088	121	6	149
Hastings River	2	1		1		+	773	8	1	22
Manning River	2	1			1		1,666	19	1	46
Port Stephens	3	1			2		420	40	10	148
Hunter River	18	4	6	8		+	3,661	564	15	1,054
Macquarie and Tuggerah Lakes	9	1	2	1	5		161	118	73	118
Hawkesbury River	80	22	26	31	1	+	3,308	1,409	43	1,614
Sydney Coast	27	16	1	5	5		288	221	79	229
Illawarra Coast	10		3	6	1		42	18	43	18
Shoalhaven River	18	5	6	6	1		1,355	1,081	80	1,090
N.S.W. South Coast	13	8	3		2	+	1,075	10	1	22
Clyde River	2	1		1		+	360	8	2	50
Bega River	5	2		3			1,955	98	5	122
Snowy River	9	3	1	5			2,779	364	13	441
Gippsland Lakes	15	2	1	11	1		4,409	2,481	56	2,497
TOTALS	293	96	56	111	30		35,082	9,258	26	11,118
PERCENT		33	19	38	10					32

* "F.C. Schemes" indicates presence of flood control scheme in system. "Weirs" <3m; "High Weirs" 3-7m; "Dams" >7m.

† "Above major barriers" includes all smoothed valley length above the most downstream dam or tidal barrier.

∞ "Above all barriers" includes all smoothed valley length above the most downstream physical barrier of any sort.

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TABLE 2. Primary purposes of impoundments in coastal drainages of south-eastern Australia.

Purpose	No. structures
Domestic and municipal	138
Riparian*	40
Electricity (hydro and thermal)	24
Irrigation	18
Mining	17
Stream gauging	16
Railways	14
Estuarine salt exclusion	9
Industry	7
Recreation	6
Unclassified	4
Total	293

* This category is made up of minor impoundments used for irrigation, stock watering, and domestic supply by riparian landholders. Included are six privately owned major farm dams, plus structures built under the N.S.W. Small Weirs Program (From records of the Water Resources Commission of N.S.W.).

OBSTRUCTED PROPORTION OF THE TOTAL HABITAT

Total smoothed valley lengths, as well as smoothed valley lengths upstream of physical barriers are listed in Table 1. Smoothed valley lengths above major barriers are also listed. Summation shows that 32% of the total habitat lies upstream of physical barriers, and 26% is upstream of major barriers.

Of the 228 streams named as "rivers" within the study area, 111 streams, or 49%, were obstructed by one or more physical barriers.

NUMBER OF MIGRATORY FISH SPECIES

Migratory patterns of the native fishes are listed in Table 3. Of 26 species that have a migratory life cycle, 11 are amphidromous, eight are catadromous, four are anadromous and three are potamodromous. Much of this classification is based on fragmentary information, including reports of accumulations of apparently migrating fish below barriers (Bishop and Bell 1978; Sloane 1980; Harris, unpublished data). Four of the fish are of economic importance; sea mullet, (*Mugil cephalus*; long-finned eel, *Anguilla reinhardtii*; short-finned eel, *A. australis* and barramundi, *Lates calcarifer*). These and seven other species; (*M. novemaculeata*; freshwater mullet, *Myxus petardi*; freshwater herring, *Potamalosa richmondia*; jungle perch, *Kublia rupestris*; Macquarie perch, *Macquaria australasica*; mangrove jack, *Lutjanus argentimaculatus*; and Australian grayling, *Prototroctes maraena*) are angling species (Lake 1978; McDowall 1980).

TABLE 3. Migration patterns of the freshwater fishes within the range of *Macquaria novemaculeata*. Species are classified mainly on the basis of the findings of the author(s) indicated by the superscript number following the species name. Species names in brackets indicate tentative inclusion in this classification.

Anadromous species	Catadromous species
<i>Geotria australis</i> ¹	<i>Macquaria novemaculeata</i> ⁵
<i>Mordacia praecox</i> ¹	<i>Myxus petardi</i> ¹⁴
<i>Mordacia mordax</i> ¹	<i>Potamalosa richmondia</i> ^{5,3}
(<i>Prototroctes maraena</i> ²)	<i>Anguilla reinhardtii</i> ⁶
	<i>Anguilla australis</i> ⁶
	<i>Lates calcarifer</i> ⁵
	<i>Galaxias maculatus</i> ⁷
	(<i>Kuhlia rupestris</i> ⁵)
Amphidromous species	Potamodromous species
<i>Mugil cephalus</i> ⁸	<i>Macquaria australasica</i> ¹²
<i>Galaxias brevipinnis</i> ⁹	<i>Leiopotherapon unicolor</i> ^{5,13,18}
<i>Galaxias truttaceus</i> ⁹	(<i>Gobiomorphus coxii</i> ^{14,3})
<i>Megalops cyprinoides</i> ¹⁵	
<i>Chanos chanos</i> ¹⁶	
(<i>Gobiomorphus australis</i> ¹⁴)	
(<i>Retropinna semoni</i> ^{17,3})	
(<i>Pseudogobius olorum</i> ¹⁰)	
(<i>Pseudaphritis urvillii</i> ¹¹)	
(<i>Notesthes robusta</i> ^{5,3})	
(<i>Lutjanus argentimaculatus</i> ⁵)	

Key to authors:

- | | |
|-----------------------------|------------------------------|
| 1. Strahan 1980a; 1980b | 10. Hoese and Larson 1980 |
| 2. Bell <i>et al.</i> 1980 | 11. Andrews 1980 |
| 3. Harris 1983b | 12. Wharton 1968 |
| 4. Humphrey 1979 | 13. Llewellyn 1973 |
| 5. Lake 1978 | 14. Hoese <i>et al.</i> 1980 |
| 6. McDowall and Beumer 1980 | 15. Pollard 1980 |
| 7. Pollard 1971 | 16. Larson 1980 |
| 8. Thompson 1954 | 17. McDowall 1979 |
| 9. McDowall 1980 | 18. Beumer 1976 |

DISCUSSION

PROPORTION OF THE HABITAT OBSTRUCTED BY IMPOUNDMENTS

All 22 drainages in the study area are impounded, and the proportion of the total aquatic habitat potentially available to fish that has been obstructed by artificial barriers is estimated at 49% and 32% by different techniques. Furthermore, some allowance must be made for the additional impact of those categories of physical barriers that were excluded from the census. Farm dams, flood control structures and road crossings are often numerous, but the few records that are kept of these structures are neither comprehensive nor readily available. Because of the ubiquity of these barriers, and as many of them prevent fish movement, their overall impact must be substantial.

It is concluded that between one-third and one-half of the habitat potentially usable by migratory fishes in coastal drainages of south-eastern Australia has been affected by the construction of physical barriers to fish passage. It is likely that the true figure lies at the upper end of this range.

However, waterfalls limit the naturally available proportion of stream length in some cases. Moreover, fish colonise different parts of the habitat, and probably only the two *Anguilla* species are to be found throughout the whole length of stream systems. The catadromous species *M. novemaculeata* and *P. richmondia* are also generally found in a major proportion of the stream length, but amphidromous species such as *M. cephalus*; bullrout, *Notesthes robusta*; or oxeye herring, *Megalops cyprinoides* only occur in lowland reaches.

Although only 13% of the exploitable yield of the water resources of south-eastern coastal drainages was being abstracted in 1977, compared with 60% in the Murray-Darling system (A.W.R.C. 1981), there has obviously been much physical interference with the migratory pathways of fishes inhabiting both of these regions.

CAPACITIES OF THE FISH TO BYPASS PHYSICAL BARRIERS

Impoundments vary greatly in their effects on migratory fish. Larvae and juveniles of catadromous fish species below low tidal barriers face an impasse of similar magnitude to that caused to adult fish by larger dams in the catchment, because swimming ability is closely related to body length (Bainbridge 1958; Blaxter and Dickson 1959). A few examples are available of the significance of this relationship. Young *L. calcarifer*, mainly under one year old, were affected by low barriers in northern Australia (Morrissy 1969); *M. cephalus*, of total length (T.L.) = 32 mm were able to ascend the Fitzroy fishway during low flows, but were prevented by higher water discharges (Kowarsky and Ross 1981); and Atlantic salmon, *Salmo salar* yearlings and juveniles were unable to pass barriers of 30 cm and 45 cm respectively (Huntsman 1945). Young *M. novemaculeata* migrate into tidal freshwater at a TL of about 12 to 20 mm, and were unable to pass a 15 cm barrier at 30 mm TL (Harris, 1983b).

Movements of fish populations may occur during flooding, but these movements are difficult to monitor under flood conditions, and little direct evidence is available. However, Llewellyn (1968) reported a marked increase in drum net catches of golden perch, *Macquaria ambigua* during floods, indicating upstream movement at this time. Also Llewellyn (1973) and Lake (1978) have noted the vigorous upstream travel of spangled perch, *Leiopotherapon unicolor* in flooded temporary channels.

Since midstream flow velocities in the neighbourhood of "drowned-out" weirs (that is, weirs carrying such a high discharge that the surface water profile is not much altered during its passage over the structure) are likely to be limiting for even the strongest swimmers, it is assumed that the slower flowing waters at the

stream margins are used for passage. This hypothesis was supported by observations of *P. richmondia* in isolated rock pools in the Clarence River gorge, high above normal river levels. Weirs and high weirs in the headwaters of streams will be drowned out more often than tidal barriers, and thus flood passage for fish will more frequently be possible in upland streams.

Seven fish species within the south-eastern Australian region are capable of climbing vertical wet surfaces, and are therefore generally less affected by physical barriers. They are the elvers of *A. australis* and *A. reinhardtii* (McDowall and Beumer 1980); the climbing galaxias, *Galaxias brevipinnis* (McDowall 1980); Cox's gudgeon, *Gobiomorphus coxii* (Bishop and Bell 1978); and the three lampreys, *Geotria australis*, *Mordacia mordax* and *M. praecox* (R. Sloane, Tasmanian Inland Fisheries Commission, personal communication).

Mugil cephalus, *Myxus petardi*, *P. richmondia*, and *Gobiomorphus coxii* can leap, and *M. cephalus* and *G. coxii* have been observed to leap to pass minor obstacles. In general, however, few Australian freshwater fishes leap, compared with Northern Hemisphere species (Stuart 1962).

Generating turbines or spillways sometimes cause substantial mortalities among downstream migrant fish (Hamilton and Andrew 1954). Outlet valves have also caused fish mortalities in some Australian dams (Eicher 1982). However, Elser (1958) has shown that fish can pass over some "free-fall" spillways without injury.

Fishways are commonly built to provide fish passage at physical barriers in other countries. But Australian fishways have seldom functioned well in the past, and very few of the 293 impoundments have been fitted with them (Beumer 1980; Eicher 1982; Kowarsky and Ross 1981; Harris 1981, and in press).

FLOOD SUPPRESSION

Flooding provides the stimulus for major events, particularly breeding or migration, in the life history of many Australian fishes. These fish include *L. unicolor* (Llewellyn 1973; Lake 1978), *M. ambigua* (Lake 1967b; Llewellyn 1968; Reynolds 1976), *A. australis* and *A. reinhardtii* (Jellyman 1977), landlocked common jollytail, *Galaxias maculatus* (Pollard 1971), *L. calcarifer* (Dunstan 1959; Morrissy 1969), fork-tailed catfish, *Hexanemichthys* sp. (Kowarsky and Ross 1981), *M. cephalus* (Thomson 1963), and *M. novemaculeata* (Harris, 1983b). Migration of salmonids is also stimulated by increased flows (Davidson *et al.* 1943; Hayes 1953). Other fish migrate in the absence of floods, including catadromous *G. maculatus* (Sloane 1980) and juvenile *M. novemaculeata* (Harris, 1983b).

Impoundments suppress downstream flooding (Walker *et al.* 1979; Baxter 1977). The 80 impoundments of the Hawkesbury River system have restricted both the frequency and amplitude of flooding (W.C.I.C. 1973). During the 1979-

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82 drought, the stored volume of water in Water Board dams on the Hawkesbury system was reduced to less than half of their capacity (J. Bellamy, Metropolitan Water, Sewerage and Drainage Board, pers. comm.).

Since flooding triggers breeding and migratory behaviour in many freshwater fish species, the alterations of hydrographic patterns caused by extensive catchment impoundment must be considered to have substantially disturbed the ecology of freshwater fish in south-eastern Australia.

WATER QUALITY EFFECTS

Water quality changes caused by impoundments may create subtler barriers to fish migration. Low temperatures and low dissolved oxygen reduce fish swimming performance (Fry and Hart 1948; Brett *et al.* 1958; Clay 1961), and alter migratory behaviour (Collins 1952; Hoar 1953). Stratified Australian impoundments have been observed to lower downstream river temperatures (Bayly and Williams 1973; Walker 1979) and dissolved oxygen (Walker *et al.* 1979); and to liberate hydrogen sulphide downstream (Hillman 1979). It is therefore reasonable to conclude that fish migrations have been affected by these changes, although definitive evidence is lacking.

Furthermore, Miles (1968) showed that an organic material was responsible for attracting migrant elvers to particular streams. This material was biodegradable, and largely broken down in three days, although some effect persisted for up to seven weeks. Detention of water in storages could therefore interfere with migrations depending on this type of olfactory guidance.

IMPACT OF OBSTRUCTED MIGRATION ON FISH POPULATIONS

Major barriers that are impassable to non-climbing fishes will eradicate local populations of the 17 non-climbers of the 23 diadromous species, at least in the upstream segment of the stream systems. Cataract Dam (49 m high), on the headwaters of the Hawkesbury River, is an example. It was sampled with gill nets on four occasions, but no diadromous species were found. Water Board employees have reported that elvers climb very high spillways, such as Warragamba Dam (94 m high), thus eels may be in Cataract Dam. Whilst none were observed, they were not specifically sought.

Catadromous populations are affected in various ways by weirs and high weirs, depending on biological factors, climate, and the characteristics of the stream and its barriers. *Macquaria novemaculeata*, *Mugil cephalus*, and *P. richmondia* are regularly found above a 2.3 m waterfall in the Clarence River, and anecdotal reports indicate the presence of *M. novemaculeata* in the Nepean River at Menangle after floods, despite the 11 weirs up to 4 m in height that are downstream of the area.

Amphidromous species whose larval and juvenile development incorporates a "whitebait" phase, such as the spotted mountain trout, *Galaxias truttaceus*

(Blackburn 1950), and possibly the striped gudgeon, *Gobiomorphus australis* (Hoese *et al.* 1980), can be eliminated from river systems by impoundments. Barriers preventing the upstream penetration of young *M. cephalus* (Thomson 1963) will restrict the production of this species by limiting its access to stream habitat.

Northern Hemisphere dams impede the downstream travel of juveniles of anadromous species (Fraser 1972b), but this problem is not known to affect Australian anadromous fish. No upstream fish passage has yet been provided past large dams, and Tasmanian smelt, *Retropinna tasmanica* and Tasmanian whitebait, *Lovettia seali* are unlikely to be affected, since they spawn in the lowland reaches of rivers (Blackburn 1950; McDowall 1979), thereby avoiding most impoundments.

The ecological significance of potamodromous behaviour in Australian fish has not yet been defined, however it is generally associated with maintenance of stable population distribution and abundance in river systems, and is a means of optimising fish production by exploiting available resources, particularly food (Northcote, 1978).

The effect of delaying migrant fish below physical barriers which may occasionally become passable varies with the maturity of the fish. High fishing mortality among adult *M. novemaculeata* was demonstrated by the return of 24.3% of tagged fish that congregated below Liverpool Weir on the Georges River (Harris, 1983b). Reports by fisheries inspectors also indicate heavy fishing mortality among *M. novemaculeata* impeded below Tallowa Dam on the Shoalhaven River, and below the Clarence River waterfall.

However, accumulations of larvae and juveniles below tidal barriers are subject to density-dependent mortality from predation. This, together with size-dependent swimming ability, is proposed as the cause of the low population densities of *M. novemaculeata* and other non-climbing diadromous fish found upstream of three tidal weirs near Sydney (Harris, 1983b). In streams having low tidal barriers, upstream catadromous populations can become dependent for recruitment upon any larger fish that may have matured in downstream tributaries or elsewhere below the tidal barrier, and can swim upstream during floods.

CONCLUSION

Continuing urban, rural and industrial development indicate that stream regulation has not yet reached its peak in south-eastern Australia. Predictions of water requirements have fluctuated considerably, but it seems certain that many new impoundments will be built (W.R.C. 1979; Richardson 1979). In considering the probable effects of this development on the native fish fauna, the more obvious impact of high dams should not divert attention from the importance of seemingly lesser barriers to migration. Neither should the migration requirements of coastal

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diadromous species be permitted to overshadow the needs of potamodromous fish for passage within stream systems.

Much of the information needed to make a precise evaluation of the status of fish in south-eastern Australian coastal drainages is still unavailable. The fish are poorly understood; only some of the types of man-made physical barriers have been listed and classified; and the many ecological effects of impoundments on fish populations require considerable further study.

Nevertheless, the preliminary work reported in this paper shows that about half the freshwater habitat that is potentially usable by migratory fishes has already been degraded or nullified by stream impoundment, and that approximately 26 species of fish are affected. These results obviously give cause for concern, and highlight the need for a much greater level of awareness and involvement in the problem on the part of environmental and water supply authorities.

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Bacterial regulation of abundance in tropical fruit flies (Diptera: Tephritidae)

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ABSTRACT

Protein bait trap and male lure trap estimates of seasonal numbers and studies on movements in several fruit fly species in southeast Queensland have led to a new understanding of the natural regulation of fruit fly abundance. Teneral female flies were observed to disperse in the company of mature males, feeding *en route* on growth flushes of highly specific leaf surface bacteria. The erratic supply of specific leaf surface bacteria in nature governs fruit fly numbers. Rainfall and temperature play only indirect roles. The supply of bacterial food for larval growth is comparatively independent of environmental parameters.

INTRODUCTION

Tephritid fruit flies devastate horticultural crops in both temperate and warmer regions of the world. In tropical and sub-tropical orchards, where most pest Tephritidae belong to the sub-family Dacinae, population outbreaks occur erratically in time and intensity. Tryon (1889) first reported increased numbers of Queensland fruit fly, *Dacus tryoni* (Froggatt), in the wake of wet summer weather. Bateman (1968) found that while temperature played a major role in the timing of stages in the life cycle of this species, the size of the resultant population was primarily a function of summer rainfall. Nishida (1963) observed a similar pattern for the melon fly *Dacus cucurbitae* (Coquillett), in India. Fitt (1981) reported a highly significant correlation between increasing rainfall and temperature and increasing trap catches of the univoltine (one generation per annum) *Dacus opiliae* Drew and Hardy in the Northern Territory during the increasing phase of the population. He explained this correlation by suggesting that flies emerging in the wet season develop a response to the male lure used in trapping. He suggested that they lose this response in the dry season, to recover it again only at the beginning of the next wet season, and that the climatic variable most likely to be involved is humidity. His trap catches of *Dacus tenuifascia* (May), however, were not correlated with temperature and rainfall. *Dacus newmani* (Perkins) of semi-arid Australia has been observed responding to male lures immediately after, and only after, significant rainfall (Courtice, unpubl. data).

Two factors have generally been employed to account for the size of wild fruit fly populations. In the first place singular emphasis has been placed on the effects of temperature on both survival and rates of development of the various stages of the life cycle. This emphasis represents the continuing influence of the work of James Davidson [1885-1945] in South Australia where extremes of temperature have an over-riding influence on insect numbers. In the second place destruction of fruit and vegetables by Tephritid larvae is always conspicuous. Thus the availability of larval host material as a factor regulating fruit fly abundance has not been neglected. These two factors were employed by Fletcher (1974). In a study of the seasonal abundance of *D. tryoni* south of Sydney, he explained population size differences between seasons and locations in terms of temperature extremes and the availability of larval hosts. As Drew and Hooper (1983) have done, he notes, but does not explain, the influence of summer rainfall.

Fruit fly numbers, however, do not always increase in the wake of summer rain. Whereas Fletcher (1974) consistently found a large peak in numbers of *D. tryoni* in autumn at all altitudes at 34°15' South Latitude, Drew and Hooper (1983), working in the Brisbane hinterland at 27°25'S found a steady decline in numbers of both *D. tryoni* and *Dacus neohumeralis* Hardy during the same months of the year. This decline occurs during the regular late summer wet season in the montane hinterland behind Brisbane. The observed decline in fruit fly numbers was greatest at an altitude of 700 m on Mt. Glorious where rainfall for the period February-April is also the greatest. At Mt. Glorious rainfall averages 647 mm for this period compared to 394 mm at Drew and Hooper's site at 100 m elevation, and compared to 226 mm and 252 mm for Fletcher's Campbelltown (55 m elevation) and Picton (168 m elevation) sites respectively.

This autumn decline in fruit fly numbers calls into question the "drinking ration" theory (Meats 1981) to account for the relation between population size and summer rainfall. Drew and Hooper's (1983) explanation in terms of the absence of larval hosts on Mt. Glorious is equally unsatisfactory. In late summer and autumn many of the rainforest trees fruit prolifically at 700 m altitude, some of them being susceptible to minor infestation by *D. tryoni* and *D. neohumeralis* (May 1953, 1957). More important, however, Golden Delicious apples in Mt. Glorious orchards ripen each year at this time and unprotected fruit is usually free from infestation. These major pest species are almost entirely dependent on exotic cultivated fruits south of the 19th Parallel of Latitude in eastern Australia (Courtice and Drew 1982).

Temperatures remain favourable for fruit fly activity on Mt. Glorious until approximately the middle of May. Food for egg production by adult fruit flies remains the variable in need of further consideration. This food requirement has been investigated primarily in relation to diets for laboratory colonies. The possibility that a shortage of adult food may influence fruit fly numbers in the field has not been investigated (Bateman 1972). Wild fruit flies have been reported

feeding on a variety of natural products, but a high protein diet commensurate in supply with the prolific egg production observed in multi-voltine pest species of the Dacinae has not been identified.

Much work has been done on fruit fly attractants, but the connection between response to these substances and the fruit fly's search for food is seldom made. Bateman (1972) treated "food" and "attractants" under different headings. Gow (1954) noted the urgent need for a more powerful attractant for females of the Oriental fruit fly, *Dacus dorsalis* (Hendel) and for flies of both sexes of *D. cucurbitae* and the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) [sub-family Trypetinae]. Neither *D. dorsalis* nor *D. cucurbitae* occur yet in Australia. Gow found that specific bacteria in the genus *Proteus* (Enterobacteriaceae) which he cultured in soy bean extract were highly attractive to these major pest species of fruit fly. Despite the fact that hydrolysed yeast protein (Steiner 1952) is the major ingredient in baits applied to orchard foliage for fruit fly control in most parts of the world, the connection between the attractancy of *Proteus* bacteria and food or other fruit fly requirements has not been further investigated. Similarly ammonia has long been used in some fruit fly lures (Perkins and Hines 1933), but even in very recent work (Bateman and Moreton 1981) the biological significance of its attractancy has remained obscure.

Gow's work was not continued and later research has been dominated by the theory that fruit flies obtain their reproductive food requirements from aphid honeydew (Hagen 1958, Neilson and Wood 1966, Bateman 1972). Recent work, however, on the feeding behaviour of *Anastrepha fraterculus* (Wiedemann) [sub-family Trypetinae] in Brazil (Malavasi *et al.*, 1983), has shown that honeydew is not a major food source for this species. Indeed the majority of the world's Tephritid fruit fly species occur in the humid tropics and sub-tropics where sooty moulds rapidly cover all homopterous secretions. The honeydew theory goes hand in hand with the theory that bacteria found in the alimentary tract of fruit flies are symbiotic. There is a large literature on the subject (Hagen 1966, Bateman 1972, Rossiter *et al.* 1982) all following Petri's (1910) interpretation of bacteria found in the oesophageal bulb of the olive fruit fly, *Dacus oleae* (Gmelin).

Although Dacine pest fruit flies occur through all but the Neotropical warmer latitudes of the world, most population studies have been carried out in Australia. It is a significant weakness of these studies that, apart from some use of sweep nets by Fletcher (1973), they have relied on data provided by the use of lures which attract only sexually mature males during seasonal periods of sexual activity. Furthermore until very recently (Drew and Courtice, in prep.) the biological significance of these lures has not been understood.

The movements of sexually mature flies have become comparatively well known. They primarily seek larval host material for their progeny and congregate in appropriate areas. Using traps (Steiner 1957) baited with cuelure (4-[p-acetoxyphenyl]-2-butanone) Courtice (unpubl. data) has repeatedly observed some

congregation of mature male *D. tryoni* and *D. neohumeralis* in peach orchards where there is ripening fruit; such congregation occurs at the expense of adjacent areas without ripening fruit. The females are readily observed among the ripening fruit. Fletcher (1973) has made similar observations at Wilton south of Sydney and the subject is well documented (Bateman 1972). In the absence of larval host material, Fitt (1981) has shown congregations of the univoltine *D. opiliae* in "dry season refuges" along forested water courses of the Northern Territory.

However the movements and congregations of teneral (immature adult) fruit flies have received little attention. They are known to disperse soon after emergence from the soil (Bateman 1972) and require food for maturation (Christenson and Foote 1960) but neither has this food been identified nor has the pattern and scale of migration been studied.

This paper presents new data on the seasonal abundance of several species of fruit fly, contradicting some aspects of current theory. Initially these data were collected in the course of observations on leaf diseases of stone fruits in the humid climate of Mt. Glorious (Courtice 1982a).

Observations on the phenomena of "succession" (Ruinen 1961) and "antagonism" (Baker and Cook 1974, Blakeman and Fokkema 1982) among leaf surface micro-organisms provided an indispensable background against which the present study was initiated. Although current observations are not pertinent to the present work, the two horticultural problems of fruit fly outbreaks and summer defoliation of stone fruits have proved to be the outcome of the same sequence of leaf surface microbial events.

MATERIALS AND METHODS

This work was carried out at Mt. Glorious (27°20'S, 152°46'E, altitude 700 m in the D'Aguilar Range of south-east Queensland. At its southern limit the suburbs of Brisbane extend to the base of this range, the upper levels of which are covered by open eucalypt and rain forests. There are some residential areas and small farms on fertile basaltic loams at Mt. Glorious. The principal experimental site was located in orchards in a rainforest clearing. This clearing occupies an isolated 20 ha plateau standing 1 km east of the main range at Mt. Glorious. Temperatures at the experimental site were measured 1 m above the ground in the total shade of a large tree on this plateau. The daily maximum temperature is normally 4-7°C lower than that recorded on the coastal plain below.

PROTEIN BAIT TRAPPING

The undersides of the leaves of a section of one grapefruit tree and one sweet orange tree were sprayed with a commercial preparation of hydrolysed protein (Roche-Maag Ltd., Sydney) [11g solids/1] plus maldison as emulsifiable concentrate [11.4g/1]. Beneath the sprayed leaves of each tree a sheet of unbleached

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calico of area 2 m² was spread. In spring 1982 these two traps were set up early in the morning of 4 September following the observation of very large numbers of *D. tryoni* and *D. neohumeralis* in a row of grapefruit trees on the previous day. On 3 September temperatures on the plateau had considerably exceeded the flight threshold of 20°C (Drew and Hooper 1983) for these species for the first time that season. In spring 1983 the same traps were set up in advance of temperatures permitting fruit fly activity at Mt. Glorious. In both years the spray was repeated at weekly intervals, or more often if rain in excess of 25 mm fell, in accordance with conventional horticultural practice for fruit fly control. During a period of dry westerly winds in October 1982 this routine was varied and foliage sprayed twice daily for five days. All fruit flies collected on the calico sheets were identified, counted and sexed. From 14 September 1983 most collections were preserved in 50% ethanol to facilitate examination of the sexual organs.

CUELURE TRAPPING

In mid-winter 1980 four traps each consisting of a horizontal 1 l cylinder of clear perspex with entrance funnels at each end (Steiner 1957) housing a wick impregnated with 4 ml cuelure + 1 ml 50% w/v dichlorvos insecticide concentrate were set up to monitor adult male numbers of those species which respond to this lure. The traps were suspended in the shade in orchard and rainforest trees approximately 200 m apart on the plateau. They were emptied daily at 700 hrs or less often when fruit fly activity was low. The traps were maintained all the year round during the period of the experiments. Occasionally in summer traps were also maintained for periods of a few weeks on Maiala Creek and on Cedar Creek above Greene's Falls at 140 m and 110 m respectively below the elevation of the plateau. All flies collected were identified and counted.

MARK AND RE-CAPTURE EXPERIMENT

On 13 November 1980, 250,000 pupae of a laboratory strain of *D. tryoni* were placed in ten 3-l plastic *jardinières*. 5 cm of sawdust mixed with rocket red fluorescent pigment (Dayglo Color Corp., Cleveland, Ohio) at the rate 10 g pigment/70 g sawdust was poured on top of the pupae. The *jardinières* were then suspended above head height from trees in dense eucalyptus forest at 100 m elevation below the eastern lip of the plateau. 1 cm wire mesh prevented interference by birds and a sticky ant barrier (Rentokil Ltd., Sydney) was smeared on the suspending wire. Many twigs were inserted through the wire mesh to enable emerging flies to climb free from their fellows and so avoid death by crowding. At emergence the flies take pigment into their head cavity on retraction of the pterinum, a balloon-like membrane which expands to break open the pupal case. The heads of re-captured flies are squashed in acetone. When it is present the pigment fluoresces under ultra-violet light. In addition to the four cuelure traps on the plateau at Mt. Glorious, 30 were set up along watercourses leading from the base of the range below the release point 25 km into the suburbs of

Brisbane. Four traps were set up on England Creek on the western side of the D'Aguilar Range to monitor flies that crossed the range.

MULBERRY FEEDING OBSERVATIONS

D. tryoni were hand collected while they were feeding on mulberry fruit in the field. They were held in glass containers, fed on brown autolysed yeast, and the time taken for the blue-purple colour of the fruit to cease in their droppings was noted. Ripe mulberry fruit were presented to caged *D. tryoni* in the laboratory. Their behaviour was observed and the time taken for blue-purple colour to appear in their droppings was noted.

MICRO-ORGANISM FEEDING TRIALS

Bacteria and yeasts were isolated from leaf surfaces and from the crops and stomachs of field collected fruit flies, and cultured on agar in the laboratory. Various preparations of these micro-organisms were then fed to caged *D. tryoni* and *Dacus cacuminatus* (Hering). The egg production and longevity of these fruit flies was then noted in comparison with the performance of flies fed on the conventional laboratory diet of autolysed yeast protein. This work is being presented as a separate paper (Drew *et al.*, 1983) although some of the results are referred to in the discussion below.

RESULTS

PROTEIN BAIT TRAPPING

A variety of insects were collected on calico sheets spread beneath baited citrus foliage. Eight species of Dacinae were represented, and one species, *Rioxa pornia* (Walker), of the Tephritid sub-family Trypetinae. Among other Diptera the families Lauxaniidae and Drosophilidae were well represented. On two occasions in spring 1982 the diversity of each day's collection was completely overshadowed by the appearance of extremely large numbers of Dacine fruit flies. These events coincided with north-west winds and temperatures on the plateau well in excess of the Dacine flight threshold of 20°C. The fruit flies were so numerous and so much confined to certain citrus trees irrespective of the presence of bait, that they assumed the character of discrete swarms. The swarm in the citrus orchard on 3 September 1982 may have comprised over 30,000 individuals. Although there was some flight from leaf to leaf and tree to tree, most individuals were preoccupied with feeding behaviour on fruit and leaf surfaces. The orchard stands in an open kikuyu grass paddock and continuous observation from the time of their arrival at about 1000 hrs through until dusk left little doubt that their sole source of food on that day lay on these fruit and leaf surfaces. Scale insects and aphids were absent. The presence of baited foliage did not appear to influence the distribution of the swarm, indicating that food as acceptable as hydrolysed yeast protein was generally available.

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The disappearance of neither swarm in spring 1982 coincided precisely with adverse weather conditions, although from 7-25 September 1982 daily maximum temperatures were well below flight threshold, falling as low as 10.5°C on 22 September. The second swarm occurred under similar conditions on 27 September 1982. Five millimetres of rain fell in a thunder shower that afternoon, followed by a dry south-west gale early on the following day. Despite favourable temperatures on 29 September the swarm was not seen again. Many of the flies collected on the calico sheets during the 1982 swarms were apparently sexually immature, as their undeveloped abdomens collapsed shortly after death. A total of 107 mm of rain was well distributed throughout September 1982. The results for this season are presented in Tables 1 and 2. Cuelure catches for the same day are given for comparison. Since the traps and sheets are cleared at 700 hrs, flies collected are always recorded as belonging to the previous day.

In winter 1983, 904 mm of rain were recorded at the experimental site for the period May-August compared with 169 mm in the same period in 1982. Only one swarm, on 14 September, was observed in spring 1983, followed by a thunder storm from the north-west at 300 hrs on the following day. Mt. Glorious was then engulfed in cloud above 600 m until a cool south-easterly change at 700 hrs caused temperatures to remain below flight threshold for several days. The swarm, however, disappeared late in the afternoon of the same day that it had arrived, more than 24 hours before the cool south-easterly change. Temperatures of 23-25°C, corresponding with 28-32°C on the coastal plain, occurred several times but no second swarm appeared. High temperatures on 3-4 October

TABLE 1. Total numbers of *Dacus tryoni* (Froggatt) plus *Dacus neohumeralis* Hardy and *Callantra aequalis* (Coquillett) collected at two protein bait traps and four cuelure traps at Mt. Glorious, August-September 1982. The protein bait traps were not set up until first light on 4 September.

Date	Daily Maximum T°C	Two Protein Bait Sheet Traps	Four cuelure traps	
			<i>D. tryoni</i> plus <i>D. neohumeralis</i>	<i>Callantra</i> <i>aequalis</i>
30 Aug.	18	—	0	0
31	19	—	6	6
1 Sep.	19.5	—	8	4
2	20	—	2	10
3	23	—	170	13
4	22.5	75	55	2
5	17	4	9	0
6	20.5	41	18	6
7	14	0	0	0
26	21	6	35	5
27	26	507	49	26
28	20.5	2	0	0
29	21	0	11	1
30	12	0	0	0

TABLE 2. Total number by sex of fruit flies collected at two protein bait and four cuelure traps at Mt. Glorious on 26th and 27th September 1982.

Trap	Species	No. males	No. females
Cuelure	<i>C. aequalis</i>	31	0
	<i>D. absonifacies</i>	5	0
	<i>D. choristus</i>	1	0
	<i>D. neohumeralis</i>	32	0
	<i>D. tryoni</i>	46	0
Protein on sweet orange	<i>D. neohumeralis</i>	92	57
	<i>D. tryoni</i>	52	39
Protein on grapefruit	<i>D. choristus</i>	1	0
	<i>D. neohumeralis</i>	86	49
	<i>D. tryoni</i>	73	64

1983 were terminated by cold wet weather for nine days during which temperatures on the plateau did not reach flight threshold. Very small numbers of fruit flies were collected after the resumption of favourable conditions on 14 October. A total of 26 mm of rain were recorded at the experimental site in September 1983 and 118 mm during the nine days commencing 5 October 1983. Results for the 1983 season are presented in Tables 3 and 4 and include the results of dissections to examine reproductive organs. Females were classed as mature if most or all of the 40-42 ovarioles which comprise each ovary contained an egg. Dissection also permitted examination of the crop and stomach which were a deep purple-blue colour when the fly had recently fed on ripe mulberry fruit surfaces. Mulberries ripen in Brisbane from the beginning of September, but not until the second half of October on Mt. Glorious, so that flies with blue-purple matter in their stomachs (Tables 3 and 4) were very recent arrivals. During the 1983 collections on the plateau, the nearest mulberry tree with ripe fruit was 2.4 km away and 350 m below the elevation of the experimental site. The range of occurrence and larval host fruits of all fruit flies collected are described by May (1963).

Feeding swarms of a small fly in the family Lauxaniidae (Queensland Department of Primary Industries Entomology Collection) were observed on several occasions in spring 1982 and 1983 and they were caught in very large numbers on the calico sheets. These Lauxaniid swarms persisted for several days and although they shared the coherence of the Tephritid swarms, they lacked the dramatic appearance and disappearance characteristic of the latter.

CUELURE TRAPPING

Figure I shows cumulative numbers of *D. tryoni* plus *D. neohumeralis* caught in four cuelure traps during three spring-summer seasons. These two species use exactly the same range of fruits for their larval hosts (May 1953, 1957). Some daily results of cuelure trapping in spring 1982 and 1983 are given in Tables 1

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and 3, although it should be noted that catches of *D. tryoni* and *D. neohumeralis* at this time are small compared to summer catches (November and December) while summer orchard fruits are ripening. During the wet season (January-March) each year numbers of these two major pest species decline rapidly. *Dacus bryoniae* (Tryon) and *Dacus choristus* (May) generally appear in increasing but still small numbers in autumn when the wet season has passed, although after a very wet winter *D. bryoniae* was relatively abundant in spring 1983. *Callantra aequalis* apparently has a lower flight threshold than the *Dacus* species observed and was caught consistently throughout all seasons whenever temperatures permitted. Cuelure catches in dense rainforest on Maiala Creek and Cedar Creek at Greene's Falls indicated a heavy traffic of fruit flies along these water courses. Catches in these traps in January were often 4-10 times greater than catches on the plateau, probably indicating a downstream movement from suburban gardens on the main ridge of the D'Aguilar Range at Mt. Glorious.

MARK AND RE-CAPTURE EXPERIMENT

The winter-spring dry season of south-east Queensland varies greatly in its intensity from one year to another. Spring 1980 was exceptionally dry and no rain was recorded at the experimental site in September that year. Light falls averaging 3 mm fell on eight occasions in October before the dry season broke on 25 October with a fall of 178 mm. Of the 125,000 male *D. tryoni* released on 8 November 1980, 123 were re-captured in the four cuelure traps on the plateau above, only 200-300 metres distant from the release point. One hectare of early season peaches on the plateau were ripe enough to attract attention from fruit flies. Nevertheless 2,127 marked flies, or 95% of all recaptures, were taken along water courses below the release point. The temporal pattern of recaptures indicated that the majority of marked flies passed 25 km down these water courses and dispersed into the suburbs of Brisbane within 3 weeks of emergence. A few were caught along the same water courses up to five months later. Only 3 marked flies were taken in the western drainage system on England Creek. Teneral flies do not respond to cuelure. No method for monitoring their movements was available in 1980 and it is assumed that the pattern of mature adult recaptures reflects the earlier movement of teneral flies. Those recaptured on the plateau may be regarded as those that did not migrate at all. (cf. Fletcher 1974).

MULBERRY FEEDING OBSERVATIONS

D. tryoni caught by hand on ripe mulberry fruit continued to pass blue-purple droppings for five hours. When ripe fruit was presented to caged *D. tryoni* blue-purple droppings appeared after two hours. The flies do not puncture the fruit. Soft fruits such as raspberry and mulberry are susceptible to leaching, especially just prior to harvest (Tukey 1971). In both cases the flies regurgitated blue-purple liquid in a series of drops on the side of the jar or cage. After 30-60 minutes had elapsed they returned to re-ingest these drops. This was followed by further regurgitation by the same fly. The process was repeated several times.

TABLE 3. Numbers of Dacine fruit flies collected at two protein bait traps, and four cuelure traps at Mt. Glorious in Spring 1983. After 13 September the number of flies containing blue mulberry dye (B) are given in parentheses. (1) *Dacus absonifacies* (May), (2) *Dacus bryoniae* (Tryon), (3) *Dacus neohumeralis* Hardy, (4) *Dacus tryoni* (Frogatt) and (5) *Callantra aequalis* (Coquillette).

Date	Daily Max. T°C	Protein Bait	1	2	Cuelure 3	4	5
31 Aug	17	0	0	0	0	0	2
1 Sep.	16.5	0	0	0	0	0	4
2	17	0	0	0	0	0	4
3	18.5	0	0	0	0	0	6
4	19.5	0	0	0	3	1	29
5	18.5	0	0	0	0	0	1
6	19.5	0	0	0	0	0	12
7	22.5	0	0	0	8	4	24
8	25	12	0	0	9	8	19
9	20	1	0	0	1	1	0
10	17	0	0	0	0	0	0
11	18	0	0	0	1	3	0
12	20.5	0	0	0	0	4	2
13	23	7	0	0	5	3	3
14	25	110(4B)	0	2	12	25	14(5B)
15	20	6	0	0	2	13	2
16	17.5	0	0	0	0	0	0
17	14	0	0	0	0	0	0
18	16.5	1	0	0	1	4	0
19	18	0	0	0	0	0	0
20	20.5	3	0	0	0	0	6
21	24	0	0	6	5	3	17
22	20	0	0	0	1	5	0
23	23	4	2	14	7	8	12(4B)
24	25.5	4	1(1B)	28(1B)	7	7	11(3B)
25	18.5	2	0	0	0	2	0
26	16	0	0	0	0	0	0
27	16.5	0	0	0	0	0	0
28	20	4	0	0	0	1	0
29	22	0	1	5	6	2	3
30	23	0	3	6	2	2	6(1B)
1 Oct.	19	0	2	6	1	4	0
2	22.5	0	2	4	1	1	5(3B)
3	23	1	3	4	4	2	4
4	25.5	5(2B)	0	3	4	10	6(1B)

DISCUSSION

In the course of two spring seasons three large swarms of fruit flies were observed at Mt. Glorious. On each occasion, despite favourable temperatures and ripe citrus fruit, the swarm disappeared as suddenly as it had arrived. This phenomenon has not been observed before in the Tephritidae. Under uniform conditions male and female *D. tryoni* each take the same time to reach sexual maturity (Drew 1969). Thus the swarms, being composed of mature males and predominantly immature females, could not have resulted from a peak emergence period during exceptionally hot weather. The seasonal sequence of larval host

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TABLE 4. Total numbers of fruit flies of each sex indicating both mature and immature forms collected at two protein bait traps at Mt. Glorious on various dates in Spring 1983. Flies were preserved in spirit and flies containing blue mulberry dye are indicated (B).

Species	Date	Immature ♂	Mature ♂	Immature ♀	Mature ♀
<i>D. halfordiae</i>	14 Sep.	0	0	1	1
<i>D. neohumeralis</i>		0	31(1B)	17	9(1B)
<i>D. tryoni</i>		0	26(1B)	16	8
<i>C. aequalis</i>		0	0	1(B)	0
<i>D. halfordiae</i>	23 Sep.	0	0	0	1
<i>D. neohumeralis</i>		0	1	0	0
<i>D. tryoni</i>		0	1	0	1
<i>D. neohumeralis</i>	24 Sep.	0	0	0	1
<i>D. tryoni</i>		0	1	0	0
<i>D. neohumeralis</i>	25 Sep.	0	1	0	0
<i>D. tryoni</i>		0	0	0	1
<i>D. tryoni</i>	3 Oct.	0	0	0	1
<i>D. tryoni</i>	4 Oct.	0	2(1B)	1	2(1B)

fruits for *D. tryoni* and *D. neohumeralis* in the Brisbane region has been described by Drew and Hooper (1983). Fruit flies in the 1982 swarms most likely emerged under loquat and mulberry trees respectively, and those in the 1983 swarm under loquat trees. Both fruit trees are numerous on the coastal plain below Mt. Glorious. Thus, although it is probable that the majority of fruit flies in each swarm emerged under one kind of fruit tree, some deliberate aggregation of mature males and immature females must have taken place to permit their arrival together on the plateau by 1000 hrs. The swarms coincided with short periods of increasing and above average temperatures. The absence of immature males in the swarm is noteworthy, and the presence of some mature females requires comment. There is little doubt that these females had been mated well before the day of the swarm. They occur in protein bait catches in small numbers throughout the season, always in roughly the same proportion to the number of males caught in cue lure traps. It is therefore suggested that mature females caught on the same day as the swarm were local flies already present on the plateau. The precise definition of sexual maturity may require further attention.

During studies on summer defoliation of stone fruit trees by fungal pathogens, Courtice (1982b) proposed that fruit flies feed on colonies of bacteria or yeasts which occur early in the seasonal succession of micro-organisms which takes place on the leaf surface. Progress in this succession, from bacteria to yeasts and then filamentous fungi, is governed largely by the age and nutritional status of the leaf (Ruinen 1956, 1961). The nutritional status of foliage generally follows an annual rhythm of accumulation and exhaustion. Whereas accumulation is largely a function of photosynthesis in the leaf and soluble nutrient accumulation in the soil, exhaustion follows growth and fruiting on the one hand, and leaching on the other.

The accumulation of soil nitrogen in regions experiencing a marked alternation between wet and dry seasons has been well documented (Birch 1958, 1959, 1960). Rapid mineralisation of soil nitrogen under a montane (seasonal) rainforest in south-east Queensland has been reported by Ian Fergus (pers. comm.). Mineralisation here takes place in concert with rising spring temperatures which permit fruit fly activity in these mountains and which possibly trigger the assembly and departure of swarms from the coastal plain. Early spring mists and thunder storms which break up the winter-spring dry season occur at the same time. Fergus found an increase from 5 to 230 ppm nitrate nitrogen in Beechmont district rainforest soil following wetting and incubation at 25°C. The bulk of the increase occurred within a few hours.

Loss of soluble nitrogen and other compounds from leaf tissue to the leaf surface, without loss to the soil below, occurs optimally in very light rain or mist (Tukey 1971). These conditions occur almost daily in some spring seasons at Mt. Glorious. Carroll (1981) found that fluxes of dissolved nitrogen on leaf surfaces were high when the tree had been exposed to substantial rainfall (more than 200 mm) during the preceeding two weeks. This condition is perhaps unnecessary at Mt. Glorious where the soil profile normally remains wet throughout the cold winter months. Carroll found that an initial pulse of leaching released dissolved nitrogen into rainwater on the leaf surface, and that important changes in microbial populations on leaf surfaces occur during the transition from a dry to a wet canopy. He estimated that the production of leaf surface micro-organisms in temperate forest was up to 175 kg/ha/year.

Bacteria occupy the first position in the leaf surface succession (Ruinen 1956). Bacterial isolation and subsequent feeding trials (Drew *et al.*, 1983) amply demonstrated that a high nitrogen leaf surface substrate can produce the normal food for Dacine, and perhaps all Tephritid, egg production. Although yeasts provoke little interest, *D. tryoni* fed vigorously on washed preparations of pure cultures of bacteria belonging to the genus *Proteus* (Enterobacteriaceae). Their egg production rose to four times that on a conventional laboratory diet of auto-lysed protein, and hatch rate rose from 75% to 97%. Longevity remained high on this diet of natural bacteria.

Rapid bacterial growth on a high nitrogen substrate normally entails some loss of ammonia gas. Ammonia and other volatile products of bacterial metabolism enable fruit flies to locate this high protein bacterial food necessary for egg production. Each species of bacterium has a specific profile of volatile metabolic emissions (Lee *et al.* 1979) and each species of fruit fly appears to seek specific bacteria. Thus some fruit flies, such as *D. bryoniae* and *D. choristus*, are more abundant in autumn than in spring on Mt. Glorious. Similarly the banana fruit fly, *Dacus musae* (Tryon), may be restricted to tropical latitudes in eastern Australia by the restricted range of its specific bacterial food. *D. neohumeralis* and *D. tryoni*, both "cuckoo" fruit flies without specific larval host fruits of their own (Courtice

and Drew 1982), differ in their ranges of occurrence in a manner which may prove explicable in terms of different adult food choices resulting from their different centres of evolution. Whereas *D. neohumeralis* inhabits New Guinea and those coastal regions of eastern Australia with most reliable humidity, *D. tryoni*, like the closely related *Dacus aquilonis* (May) of the Northern Territory, is common where an acute dry season prevails for some part of most years.

Whereas leaf surface acidity (pH 6-6.5) generally favours bacterial growth, fruit surfaces are usually more acid (pH 3-4) and provide a suitable substrate for yeasts and fungi (Dennis 1976). The means by which female fruit flies locate their larval host fruits is not yet known. Once the fruit has been discovered, however, female *D. tryoni* and *D. neohumeralis* have been observed "feeding" on the host fruit surface in the same place that the ovipositor is then inserted (Tryon 1889). Norman Jones (pers. comm.) has observed *D. tryoni* "spitting" on fruit prior to oviposition.

We submit that there are two kinds of bacterium used by Tephritid fruit flies. One kind feeds the adult and the other feeds the larvae. Larval food bacteria have been shown to cause fruit rotting (Rossiter *et al.* 1982) and these bacteria may be isolated from the oesophageal bulb of the adult. This small appendage to the oesophagus of Tephritid fruit flies has been illustrated in Drew *et al.* (in press). By means of regurgitation onto fruit surfaces and subsequent oviposition through the droplet of "spittle" observed by Jones, the female introduces these bacteria with her eggs into the host fruit. The events of fruit rotting and egg hatch may be triggered by pH changes in the ripening fruit. Newly hatched larvae tunnel to the centre of the fruit, no doubt spreading bacteria as they go, and then feed their way back towards the outside again. They feed upon bacteria and not, as commonly supposed, upon fruit tissue. The brown bacterial "soup" familiar in infested fruit is always in front of them as they feed, not behind them. It has been demonstrated that these bacteria are retained from the larval stage in the oesophageal bulb of the pupa and are thus passed on to the newly emerged adult (Tsiropoulos 1976). Petri (1910) believed mistakenly that the bacteria found in the oesophageal bulb of adult *D. oleae* were symbionts rather than food for their larval progeny. This belief has persisted (Rossiter *et al.* 1982). Fitt (1983) has fed and raised fruit fly larvae on one such bacterium. The repeated regurgitation and re-ingestion of mulberry juice by *D. tryoni* suggests the means by which the supply of oesophageal bulb bacteria is maintained. Thus the numerous observations of fruit flies feeding on leaf surfaces on the one hand, and fruit surfaces on the other, may be understood.

Bacteria hydrolyse leaf surface proteins for adult fruit flies and fruit tissue proteins for larvae. Drew (unpubl. data) has shown that fruit tissue infested with fruit fly larvae contains at least twice the amount of each amino acid, essential to these fruit flies, as is found in uninfested fruit tissue. Hydrolysed protein is essential in the diet of both larval and adult fruit flies (Bateman 1972, Hagen 1953). The crop and stomach of larval and adult fruit flies is very acid (pH 3)

(Drew *et al.* 1983). The acid conditions not only confirm that bacteria cannot grow in these organs, as symbiotic bacteria would need to do, but also indicate that the flies do not contain proteinase enzymes to hydrolyse ingested protein. Most insect proteinases are active under neutral or alkaline conditions (Gilmour 1961). Fitt (1983) has shown that bacteria that secrete proteinases, when fed to fruit fly larvae, are pathogenic and destroy the stomach wall. Since hydrolysed protein is essential in the diets of both adults and larvae, it seems most likely that these are ingested through a diet of bacteria which autolyse in the acid conditions and release their cell contents into the alimentary canal.

The conditions which promote the growth of leaf surface bacteria at Mt. Glorious are clearly transitory. By mid-summer filamentous fungi become dominant on leaf surfaces of stone fruit trees and foliar applications of inorganic nitrogen are required if susceptible cultivars are not to succumb to pathogens which mark the end point of the succession on these trees. Although ornamental peach trees are very numerous in the Brisbane region, and are always heavily infested by *D. tryoni* and *D. neohumeralis*, increases in fruit fly numbers at Mt. Glorious, following their emergence in January, are usually small (Fig. 1). Both the movement of marked flies away from the mountain and the absence of a second spring swarm after the very wet winter of 1983 suggest that teneral fruit flies migrate towards regions having a recent history of drought and concomitant accumulation of soil nitrogen.

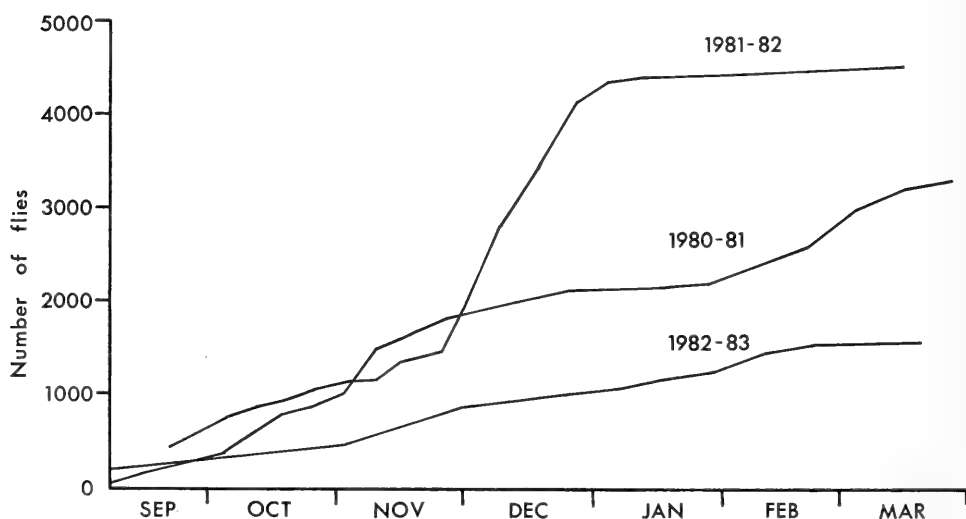


Fig. 1. Cumulative totals of *Dacus tryoni* (Froggatt) plus *Dacus neohumeralis* Hardy caught in four cue lure traps on Mt. Glorious during the 1980-1, 1981-2 and 1982-3 spring-summer seasons.

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It is unreasonable to expect multi-voltine fruit flies such as *D. tryoni*, *D. neohumeralis*, or *D. dorsalis* to be sedentary. Just as the multi-voltine fruit fly relies upon a sequence of host fruits through the season, such species also rely on a sequence of high nitrogen feeding conditions for each cycle of egg production. In the humid tropics leaf surface nitrogen fixing bacteria in the genus *Beijerinckia* are widespread and constitute the principal nitrogen source for tropical rainforest (Ruinen 1956). In Australia, away from affluent suburban conditions where soil and plant nitrogen are sustained at high levels for long periods by artificial means, a high nitrogen leaf surface substrate depends on soil fertility and a prior history of even short-term drought followed by rainfall and humidity (Birch 1958 *et passim.*). Erratic rainfall and disastrous drought are ever-recurring themes over most of Australia (Leeper 1960), and a capacity for long distance migration is characteristic of much of the fauna of the continent.

The repeated occurrence of swarms of the small Lauxaniid fly (D.P.I. Entomology Collection) throughout spring suggested that the brief passage of fruit fly swarms on Mt. Glorious was not immediately related to the exhaustion of their food supply. It is suggested that they moved on as discrete swarms along a migration route to drier places, perhaps breaking up only as the females reach sexual maturity, then to continue individually until larval host fruits are discovered. Fruit flies may travel considerable distances down the western rivers of Queensland and New South Wales (Courtice and Drew 1983, J. R. MacFarlane unpub. data) and may be sustained on these journeys by homopterous secretions in the *Eucalyptus* flora which lines the river banks all the way to South Australia. *Callantra aequalis* frequently appeared on Mt. Glorious early in the day after feeding on the surface of mulberry fruit on the coastal plain a short time before. Although the larval host of this species (May 1957) is confined to rainforests on the eastern side of the Great Dividing Range, one specimen was taken (Courtice) in Autumn 1983 near Goondiwindi, 240 km down the MacIntyre River west of the watershed of the Great Dividing Range. Two specimens of *D. cacuminatus*, almost equally remote from their nearest larval host fruit, were taken at the same place and time. Specimens of *D. cacuminatus* have been collected in male lure traps on the Murray River at Albury, 250 km due west of the nearest larval host plant. Specimens of *Dacus jarvisi* (Tryon) were collected on 6 April 1983 in a station garden citrus tree 400 km south of Katherine in the Northern Territory (Allan Allwood, pers. comm.). These flies were perhaps 500 km from their nearest larval host tree.

CONCLUSION

Adult food for fruit flies occurs on leaf surfaces in erratic supply according to periodic accumulations of soil nitrogen and subsequent conditions which favour the growth of leaf surface micro-organisms. Although it may influence the number of generations in a season (Meats 1981), temperature cannot provide a guide to the size of the resultant population. The East Australian Current, flowing south from equatorial regions at 4 knots, maintains equitable temperatures for fruit

fly activity throughout much of the year in coastal regions of the eastern continent. The temperature extremes which dominate insect life in South Australia are generally absent. Apart, then, from some seasonal regulation of generation times, and given the present-day widespread occurrence of exotic larval host trees together with the fruit fly's capacity for rapid long distance migration, these studies indicate that a food supply for egg production is the factor primarily responsible for fluctuations in numbers of *D. tryoni* and *D. neohumeralis*, the two major pest species in eastern Australia.

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Descriptive notes on the fauna and flora of Merimbula, Pambula and Back Lakes, New South Wales

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ABSTRACT

An annotated list of animals and plants occurring in the estuarine areas of Merimbula, Pambula and Back Lakes is provided together with information on their abundance and habitat. Notes on the physical environment of these estuarine areas are also given. A brief synopsis of previous studies in the area is given and the distribution of the fauna and flora is compared to other estuarine areas in Eastern Australia.

INTRODUCTION

The few published surveys of New South Wales estuaries have concentrated on the distribution of the major components of the flora and some components of the fauna. The general distribution of mangroves along the New South Wales Coast is reported by Saenger *et al.* (1977) but detailed distributions within an estuary are unavailable for most regions. Areas for which detailed information is available include Towra Point, Botany Bay (Australian Littoral Society, 1977), Sydney region (Blacker, 1977); Fullerton Cove, Hunter River (Hutchings, 1983); Kooragang Island, Hunter River (Moss, in press). Detailed information on the distribution of seagrass beds and mangroves is currently being prepared for each estuary by the New South Wales Division of Fisheries and will be published as technical reports by West *et al.*

Estuarine fauna has in contrast been subjected to a far less co-ordinated approach. Several studies have concentrated on the fauna of restricted areas: Gunnamatta Bay and Cabbage Tree Basin, Port Hacking (Rainer, 1981); Careel Bay, Pittwater (Hutchings and Recher, 1974), Hawkesbury River (Hutchings *et al.* 1977); Gosford Lagoons (Weate and Hutchings, 1979). Recently Hutchings and Murray (in press) have described the polychaete fauna of estuarine areas in New South Wales. Broad scale surveys by the Australian Museum (1977), and CSIRO, Division of Land Use Survey of the South Coast of New South Wales (Anderson *et al.*, 1981) collected some information on the distribution of the larger benthic organisms.

Hutchings and Recher (1982) have tried to collate all the existing data on the fauna of New South Wales mangroves and have compared it to other mangrove areas. Much of this data is anecdotal and often material was not deposited in Museums for later verification. This is critical as in many of the groups considerable taxonomic confusion exists.

Quantitative data on estuarine fauna is lacking. Collett *et al.* (in press) have sampled the fauna of *Posidonia* seagrass beds along the New South Wales coast. Quantitative data is available from Botany Bay (Australian Littoral Society, 1977; State Pollution Control Commission, 1978, 1979a, b, c, 1980, 1981a, b, c; Jones, 1981; Jones and Caddy, 1981). Detailed studies are currently being carried out on the benthos of the Hawkesbury River by Jones of The Australian Museum (in press).

This lack of basic data on the distribution and abundance of estuarine flora and fauna, and the virtual absence of data on life histories, secondary productivity, etc., impose severe constraints on the development and implementation of management plans for estuarine areas in New South Wales. Collett and Hutchings (1977) have shown that many conflicting activities occur within estuarine ecosystems. Management is essential but currently lacking in most estuarine areas.

The purpose of this survey of Merimbula and associated areas was to provide some baseline data on a relatively unmodified south coast estuary and to compare it with other estuarine areas along the east coast. This paper deals only with the distribution of the fauna and flora. A subsequent paper will deal with the seasonal and quantitative aspects of the fauna along the four intertidal transects sampled.

STUDY AREA

Merimbula estuary extends from 36°53' to 36°55'S latitude and 149°52' to 149°55'E longitude (Fig. 1). Merimbula estuary is referred to as Merimbula Lake and covers an area of 5.6 km² and is divided into two by the Princes Highway bridge; Top Lake on the western side and East Lake on the seaward side of the bridge. The catchment, predominantly woodland, covers an area of 42 km² and is drained by Boggy Creek which flows into Merimbula Lake by a delta at the western end.

Mangroves and sedges occur in the delta of Boggy Creek. Seagrass beds (*Posidonia*, *Zostera* and *Halophila*) are found in the eastern half of Top Lake and along the southern shores of East Lake. A maximum depth of 9 m occurs in the centre of Top Lake. Merimbula Lake is permanently open to the sea, but the channel is only 2 m deep and is constricted by a sandspit which encroaches from the south. The estuary is marine with salinities ranging from 26.5-35.5‰ and an annual surface water temperature range of 9-24°C.

DESCRIPTIVE NOTES ON FAUNA AND FLORA

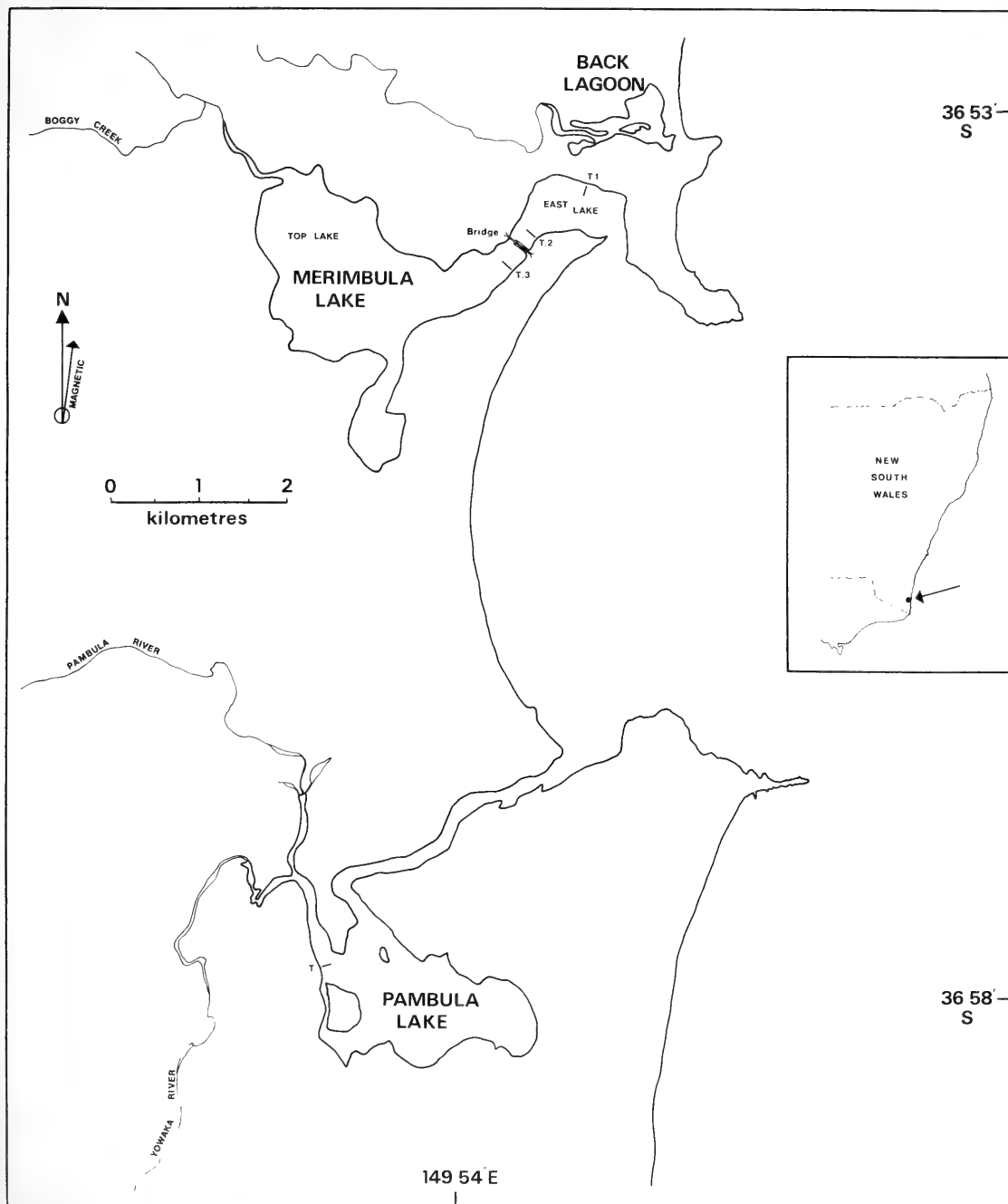


Fig. 1. A map of the study area showing transect sites. T1 Spencer Park, T2 South Bank 200 m seawards of bridge, T3 Top Lake 300 m above the bridge T = Pambula Lake.

Although the main survey was concentrated in Merimbula Lake, we also sampled in nearby Pambula Lake and Back Lake (also known as Back Lagoon). Pambula Lake is 9.6 km south of Merimbula, with a catchment of 270 km². Two rivers drain into the estuary, the Yowaka and the Pambula. River flow in the Yowaka can be fast and the river banks are steep and eroded whereas the Pambula is slow flowing. Both rivers flow into Saltwater Creek before entering Pambula Lake. The lake is about 3 km² in area, 100-200 m wide and up to 3 m deep, with many sandy shoals and rocky outcrops. It is permanently open to the sea. The salinity in the lake is usually above 30‰, but Saltwater Creek has a more varied salinity (depending on the rainfall) from 0-28.7‰ often with layering. Extensive *Zostera* beds, and a mangrove island of *Avicennia* with patches of salt marsh, occur in the lake.

Back Lake lies just north of Merimbula and is fed by a small stream draining a catchment of 33 km². The stream flows through marshes before entering the western end of Back Lake.

The lake is about 0.3 km² in area. It is normally closed to the sea, but after heavy rain the lake rises rapidly and the entrance is bulldozed to prevent flooding of surrounding farmland. When open to the sea, the spring tidal range within the lake is about 1 m. The western margins of the lake are muddy with *Juncus* and other sedges along the waterline. Patches of *Zostera* occur near the seaward entrance on muddy sand, but the entrance is clean sand.

During the study period, Back Lake was open during July, 1975, but then closed for 5-6 months until being opened again artificially in early March, 1976. When the lake is closed to the sea the salinity falls and the water level stabilizes above the tidal high water mark.

SAMPLING METHODS

Sampling was carried out at 3 monthly intervals from July, 1975 to March, 1976. Three intertidal transects were surveyed in Merimbula Lake (Fig. 1): T.1 Spencer Park, 0.6 km from the mouth, T.2 South bank, 200 m seaward of bridge and T.3 Top Lake, 300 m above the bridge. The transects were chosen as being representative of the intertidal environments in the lake. At each of the four to six stations on each transect, two cores of 0.11 m² area and 0.25 m depth were collected and sieved through a 1 mm mesh screen.

Subtidal fauna was sampled qualitatively using SCUBA and by a Smith-McIntyre grab along the main channel of East Lake and in the *Posidonia* and *Zostera* seagrass beds along the southern shores of East Lake. Qualitative plankton trawls were taken underneath the Princes Highway Bridge at each sampling period. The pelagic fauna was sampled qualitatively by pulling nets of varying mesh sizes through the *Posidonia* and *Zostera* seagrass beds along the southern shores of East Lake. Qualitative collections were also made in the mangroves and

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salt marshes in the southern area of Top Lake west of the airstrip, in the salt marshes at the entrance of Boggy Creek and along the rocky shores at the seaward end of East Lake.

Sediment samples were collected from each station on the transects and at various points along the estuary.

In Pambula Lake, quantitative intertidal collections were made across a sand bank as indicated in Fig. 1, and qualitative sampling was carried out in several habitats including rocky intertidal areas at the seaward entrance to the Lake, *Zostera* seagrass beds, *Avicennia* mangroves and the salt marsh communities. In Back Lake, all sampling was qualitative and the following habitats were sampled; intertidal beaches both of clean sand and muddy sand, *Zostera* seagrass beds, and salt marsh and sedge communities at the head of the estuary.

Material has been deposited in The Australian Museum.

RESULTS

A. SEDIMENT CHARACTERISTICS

Top Lake

The silt content (0.1%) and the median particle size of sand ($Md = 0.35$ mm) are fairly constant throughout the lake, however the proportion of organic carbon increases from the shoreline to the deepest areas where it reaches 7.3%. Dead bivalve shells are common in the deeper areas. The exit channel from the bridge is clean sand ($Md = 0.30$ mm) with patches of gravel.

Merimbula Lake Region

The channel bed in East Lake consisted of loose stones, broken shells and a mixture of coarse and medium sand, median grain size (Md) values range from 0.53-2.98 mm, sorting coefficient (QDg) values from 0.15-0.39 and skewness (Sk) values of 1.06 or greater. Silt was absent and organic carbon averaged 0.1%. The sediment among the *Zostera* and *Posidonia* beds was medium sand ($Md = 0.34$ mm) with little silt.

Sediments in the three transects were as follows:

T.1 — Medium sand, marine in origin ($Md = 0.35$ -0.4 mm) with stones and gravel from the embankment at high water mark. Silt (1.6%) and organic carbon (1.3%) accumulate in the depression in the lower part of the transect.

T.2 — Medium to fine sand ($Md = 0.28$ -0.30 mm) with little silt (0-0.2%) and an accumulation of organic carbon at the low water mark (1.3%).

T.3 — Ranges from clean medium sand ($Md = 0.34$ mm) at high water mark to mud ($Md = 0.30$ mm, 1.1% silt and 0.4% organic carbon) at low water mark.

The sediments are sharply delineated into marine deposits on the shallow banks which extend to the middle of Top Lake and the fluvial deposits extending

from the deep part of Top Lake to Boggy Creek. The marine deposits are characterised by very little silt, or organic carbon, but relatively large amounts of calcium carbonate, up to 2.22%. Fluvial deposits in comparison contain more silt and organic carbon with the highest concentration (7.3%) occurring in the deeps of Top Lake and very low levels (0.07%) of calcium carbonate.

B. FLORA

On the foreshores of Merimbula Lake, the following salt marsh plants occur: *Sporobolus virginicus*, *Juncus kraussii*, *Spergularia rubra* and *Selliera radicans*. *Triglochin striata* occurs in seepage areas. Dense stands of *Sarcocornia quinqueflora* occur at neap high tide in some places. Dense patches of shrub-like *Avicennia marina* less than 4 m high occur, sometimes forming thickets 20 m in depth. At the mouth of Boggy Creek, the mangroves form denser stands and trees reach a maximum height of 5 m. *Avicennia* is abundant, and *Aegiceras corniculatum* common. The salt marsh is well developed with tall stands of sedge *Scirpus "maritimus"* on the saline mudflats, and *Typha* sp. and *Phragmites australis* occur higher up the creek.

The algae *Enteromorpha* and *Ulva* are common from low to mid water mark throughout the estuary. Other species such as *Cladophora* sp., *Hormosira banksii*, *Codium* sp. and *Lophosiphonia* sp. occur on oyster racks, and along the channel. *Codium* sp. and *Sargassum* sp. are abundant on boulders below low tide. Fine filamentous algae occur as epiphytes on the sea grasses, but these were not identified. Extensive beds of seagrasses occur throughout the estuary except for the channel and the deeper parts (5-9 m) of Top Lake. Intertidally and down to extreme low water spring, *Zostera capricorni* and *Z. muelleri* occur with *Z. capricorni* being dominant. Below the *Zostera*, *Posidonia australis* occurs to 3-4 m. Interspersed with *Zostera* and *Posidonia*, is *Halophila ovalis*.

C. FAUNA

Tables 1, 2 and 3 provide annotated lists of the fauna and flora of Merimbula, Back Lake and Pambula Lake together with an indication of the abundance.

An extensive quantitative sampling program of the benthos of the *Posidonia* seagrass beds in East and Top Lake was carried out as part of a survey of the benthos of *Posidonia* along the New South Wales coast. An analysis of the results including a species list is given by Collett *et al.*, (in press).

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TABLE 1. Annotated list of aquatic macrophytes and invertebrate animals recorded in Merimbula, Pambula and Back Lake estuaries. Species marked with an asterisk were found in quantitative samples from intertidal muddy sand or in 0.1 m² cores from subtidal sea grass beds. Relative abundance in this list is shown by P — rare or doubtful; F — fairly common; C — common; A — abundant; N — numerous records.

Species	Merimbula					Back Lake	Pambula estuary	Remarks
	Nos. recorded	Intertidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal			
	1	2	3	4	5	6	7	8

ALGAE								
<i>Acetabularia</i> sp.	1			P				
<i>Cladophora</i> sp.	10		C			C	C	
<i>Codium</i> sp. (arborescent)	4				P			
<i>Codium</i> sp.	N				C			
<i>Codium</i> sp. (prostrate)	2	P						
<i>Enteromorpha</i> sp.	10		A		A	A	A	
<i>Colpomenia sinuosa</i> (epiphytic)	4				C			on <i>Zostera</i>
<i>Dictyota</i> sp.	4				C			on <i>Posidonia</i>
<i>Hormosira banksii</i>	10		A					
<i>Sargassum</i> sp.	5				F			
<i>Laurencia</i> sp.	6				C			on <i>Zostera</i> and <i>Posidonia</i>
<i>Lophosiphonia</i> sp.	N				C			
<i>Polysiphonia</i> sp.	3				F			on <i>Posidonia</i>
nr. <i>Thuretia</i> sp.					P			
<i>Ulva</i> sp.	10		A		A			

ANGIOSPERMS								
<i>Aegiceras corniculatum</i>	1			F				in Boggy Creek
<i>Avicennia marina</i>	10			A			A	
<i>Cotula coronopifolia</i>	1					P		
<i>Halophila ovalis</i>	15	A			A			
<i>Juncus kraussi</i>	6				A	A	A	
<i>Phragmites australis</i>	2			A			A	
<i>Posidonia australis</i>	15				A		P	
<i>Sarcocornia quinqueflora</i>	5			A		C	P	
<i>Sarcocornia</i> (bushy) (= <i>Arthrocnemum</i>)	3				C	C		
? <i>Scirpus maritimus</i>	2				P			
<i>Selliera radicans</i>	1				P			
<i>Spergularia rubra</i>	1				F			
<i>Sporobolus virginicus</i>	6	C			C	A	A	
<i>Triglochin striata</i>	2				F		F	
<i>Typha</i> sp.	2				P			low salinity to FW.
<i>Zostera capricorni</i>	15	A				A	A	
<i>Zostera muelleri</i>	2	?C			?		?	not distinguished in field

Species	Nos. recorded	Merimbula	Back Lake	Pambula estuary	Remarks			
	1	Intertidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal	6	7	8
<hr/>								
PORIFERA	4							
<hr/>								
CNIDARIA								
Actinia ?tenebrosa	5		P				F	
?Hydractinia	5				F			on Nassarius jonasii
?Edwardsiidae*	15	P			P			
<hr/>								
PLATYHELMINTHES: TURBELLARIA	6							
<hr/>								
NEMERTINA	31						1	
<hr/>								
PHORONIDA								
Phoronis albomaculata*	11	F			F			
Phoronis psammophila*	8	F			P			
Phoronopsis harmeri*	12	C			F			
<hr/>								
SIPUNCULA								
Phascolosoma annulatum*	6	P			P			
<hr/>								
POLYCHAETA: ERRANTIA								
Ancistrosyllis cf. constricta	2	P			P			
Australonereis ehlersi*	12	A				C		P
Brania clavata*	1	P						
Ceratonereis pseudoerythraeensis*	18	A			C	P		F
Ceratonereis mirabilis*	11	C			F			
Eulalia (Eumida) sanguinea*	4	P						
Eunice antennata*	2	P			P			
Exogone cf. verugera*	1	P						
Glycera americana*	3	P			P			
Glycera tessellata*	2	P			P			
Harmothoe praeclara*	28	C			C			on Zostera
Lumbrineris coccinea*	2	P				P		
Lumbrineris latreilli*	30	C			A			
Lumbrineris tetraura*	9	P			F			
Lysidice natalensis*	1		P					
Marphysa macintoshi*	1			P				
Marphysa sanguinea*	2	P			P			
Nematonereis unicornis*	1	P						
Nephtys australiensis*	115	A			C	C		A
Nephtys longipes*	9	F						
Nereis (Neanthes) acuminata	1				P			
Nereis (Neanthes) vaalii*	5		P					
Ophiodromus sp. 1*	10	P			P			
Paralepidonotus ampulliferus	1		P					
Perinereis nuntia brevicirris*	6	F				P		P under stones
Perinereis obfuscata*	2	P						

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Species	Merimbula				Back Lake	Pambula estuary	Remarks	
	Nos. recorded	Intertidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal			
	1	2	3	4	5	6	7	8
<i>Phyllodoce (Anaitides)</i>								
<i>?australis*</i>	12	P			P	P	P	
<i>Pionosyllis ehlersiaeformis*</i>	1				P			
<i>Platynereis australis*</i>	2	P						
<i>Platynereis dumerilii*</i>	3				P			on <i>Zostera</i>
<i>Progoniades</i> sp. 1	1						P	
<i>Protodorvillea</i> sp. 1*	1	P						
<i>Pseudonereis variegata</i>	1		P					
<i>Schistomeringos rudolphi*</i>	6	P			P			
<i>Sigalion ovigerum*</i>	20	F				P	P	
<i>Sphaerosyllis semiverrucosa*</i>	1	P						
<i>Syllis (Typosyllis) armillaris*</i>	2	P			P			
<i>Syllis (Typosyllis) hyalina*</i>	2	P						
POLYCHAETA: SEDENTARIA								
<i>Aonides oxycephala*</i>	5	P			P			
<i>Armandia intermedia*</i>	18	F			F			
<i>Barantolla lepte*</i>	49	C			C	P	P	
<i>Boccardia chilensis</i>	4		P			P	P	
<i>Capitella capitata*</i>	4	P			P			
<i>Caulerella tricapitata*</i>	1	P						
<i>Chaetopterus variopedatus</i>	1	P						
<i>Cirriiformia chrysoderma nuchalis*</i>	9	F			P			
<i>Cirriiformia filigera*</i>	22	A						
<i>Cirriiformia tentaculata*</i>	39	F			A			
<i>Euclymene trinalis*</i>	1	P						
<i>Ficopomatus enigmaticus</i>	1						F	in low salinity
<i>Galeolaria caespitosa</i>	8		A				A+	+ near Pambula mouth
<i>Heteromastus filiformis*</i>	15	F			F			
<i>Janua (Dexiospira) brasiliensis</i>	6				A			on <i>Zostera</i> and <i>Posidonia</i>
<i>Janua (Dexiospira) steueri</i>	1			A				on <i>pneumatophores</i>
<i>Magelona</i> cf. <i>pitelkai*</i>	13	P			F	P		
<i>Mediomastus californiensis*</i>	21	C			C			
<i>Mesochaetopterus ?sagittarius*</i>	1				P			
<i>Terebella</i> sp. nov.*	14	F	P					
<i>Notomastus torquatus*</i>	10	F		P	P	P	P	
<i>Owenia fusiformis*</i>	26	F		P			F	
<i>Phylo felix</i>	1				P			
<i>Pista typha*</i>	33	C			C			
<i>Polydora socialis*</i>	13	F						
<i>Polyopthalmus pictus*</i>	2	P						
<i>Pomatoceros caeruleus</i>	3		P		P			
<i>Prionospio (Aquilaspio) aucklandica*</i>	9	P			C			
<i>Prionospio (Aquilaspio) multipinnulata*</i>	3				P			

Species	Merimbula					Back Lake	Pambula estuary	Remarks
	Nos. recorded	Intertidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal			
	1	2	3	4	5	6	7	8
<i>Prionospio (Minuspio) cirrifera</i> *	9	P			P			
<i>Pseudopolydora kemp</i> i	15	C					P	
<i>Rhinothelopus macer</i>	1				P			
<i>Samythella</i> sp.*	1	P						
<i>Scoloplos cylindri</i> fer*	1	P						
<i>Scoloplos simplex</i> *	27	C				C	P	
<i>Spio pacifica</i> *	2	P						
<i>Terebella</i> cf. <i>ehrenbergi</i> *	3	P	P					
CIRRIPIEDIA								
<i>Balanus amphitrite</i>	2					P	P	
<i>Balanus variegatus</i> var. <i>cirratus</i>	1		P					
<i>Balanus trigonus</i>	1		P					
<i>Chthamalus antennatus</i>	4		P				P	
<i>Elminius modestus</i>	12		A			A	A	
<i>Tetractitella purpurascens</i>	1		F					
AMPHIPODA								
(incompletely identified)								MER No. is reference specimen
<i>Aora</i> MER 312 H	1			P				
? <i>Aoroides</i> * MER 148 Y	6	P		P				
<i>Atylus</i> MER 305 E	1						P	
? <i>Corophium</i> * MER 93 K	5	P		P				
<i>Cymadusa</i> sp. 1* MER 93 J	43	C		A			C	in sea grasses
<i>Cymadusa</i> sp. 2* MER 275 Y	9			C			P	in sea grasses
<i>Exoedicerus fossor</i> *	75	A			P		F	intertidal
<i>Exoedicerus</i> sp.* MER 56 C	1	P						
Eusiridae ? gen MER 301 J	2			P				
Haustoriidae gen. M*								
MER 3 D	9	F						
Haustoriidae gen. N.								
MER 163 D	1	P						
Isaeidae* MER 249 E	3	P						
<i>Limnoporeia yarragae</i> *	1	P						
<i>Maera</i> sp. MER 289 L	1			P				
? <i>Megamphopus</i> * MER 93 P	12	P		P				in <i>Zostera</i>
<i>Melita</i> sp. * MER 42 D	17	P		P	P		P	in <i>Zostera</i>
? <i>Monoculodes</i> * MER 195 N	12	C						in <i>Zostera</i>
Oedicerotidae sp. A*								
MER 207 K	5	F						
Oedicerotidae sp. C*								
MER 220 Z	5	F						
Oedicerotidae sp. 1								
MER 275 O	1	P			P			
Oedicerotidae sp. 2*								
MER 279 D	3		P					
<i>Orchestia chilensis</i> MER 5 A	2	P						drift weeds at HWS

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Species	Merimbula					Back Lake	Pambula estuary	Remarks
	Nos. recorded	Inter tidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal			
	1	2	3	4	5	6	7	8
<i>Orchestia</i> sp. MER 96 E	8	P				C	P	at HWS
<i>Paracalliope</i> sp.* MER 24 D	7	P			P			in weed beds
Phoxecephalidae A*								
MER 241 C	46	A			A		P	in <i>Zostera</i>
Phoxecephalidae B*								
MER 275 P	31	A						in <i>Zostera</i>
? <i>Podocerospis</i> sp.*								
MER 73 F	2	P			P			
? <i>Talitroides</i> MER 172 A	1	P						HW drift weed
<i>Talorchestia</i> sp. MER 308 B	5	F						HW drift weed
<i>Tethygeneia</i> sp.	1	P						in <i>Zostera</i>
<i>Urohaustorius metungi</i> *	24	A					P	
<i>Victoriopisa</i> sp.	1						P	
ISOPODA								
<i>Actaccia pallida</i> *	88	A				F	F	sand at HW
<i>Ancinus</i> sp. MER 307 D	2						F	in low salinity
<i>Cirolana</i> cf. <i>arcuata</i> *	68	A					F	
<i>Deto marina</i>	2			P			P	
<i>Exosphaeroma laevis</i>	2					P	P	on rock near mouth
<i>Cymodoce</i> sp. MER 307 C	2						P	in low salinity
<i>Codonophilus</i> cf. <i>imbricatus</i>	1				P			fish parasite
<i>Ligia australiensis</i>	1			P				on log
<i>Mesanthura</i> sp.* MER 272 Q	1	P						
<i>Nerocila macleayi</i>	1				P			fish parasite
<i>Paridotea unguolata</i>	4	P			P			on <i>Zostera</i>
<i>Sphaeroma quoyanum</i>	1						P	on rotten log
Sphaeromatidae ? gen.								
MER 304 D	5						C	in low salinity
TANAIDACEA								
	4							
CUMACEA								
	5							
LEPTOSTRACA								
	6							
MYSIDACEA								
<i>Gastrosaccus dakini</i> *	6	P					P	weed beds and plankton
DECAPODA: MACRURA								
<i>Alpheus</i> sp.*	31	F			F	P	P	<i>Zostera</i> beds
<i>Macrobrachium intermedium</i>	20				A		A	netted in <i>Zostera</i> beds
<i>Palaemon affinis</i>	1				P			netted in <i>Zostera</i> beds
<i>Penaeus plebejus</i> (juveniles)	22	P			P		P	in <i>Zostera</i> beds

Species	Nos. recorded	Merimbula	Back Lake	Pambula estuary	Remarks			
	1	2	3	4	5	6	7	8
<i>DECAPODA ANOMURA</i>								
<i>Callianassa arenosa</i> *	12	F			P	A	P	in mud
<i>Callianassa australiensis</i>	6	F				P	C	in sand
<i>Diogenes custos</i> *	5	F						
<i>DECAPODA BRACHYURA</i>								
<i>Australoplax tridentata</i>	4						A	mangrove mud
<i>Brachynotus spinosus</i> *	2	P	P					
<i>Carcinus ?maenas</i> *	6	P			P			
<i>Cyclograpsus audouinii</i>	2		P					
<i>Halicarcinus cf. ovatus</i> *	14	P			P		P	
<i>Halicarcinus paralacustris</i>	17	F			P		P	
<i>Heloecius cordiformis</i>	4			F			F	
<i>Helograpsus haswellianus</i>	4			C			C	
<i>Macrophthalmus latifrons</i>	1					P		
<i>Macrophthalmus setosus</i>							P	
<i>Macrophthalmus tasmanica</i>						P		
<i>Mictyris longicarpus</i> *	60	A					F	
<i>Mictyris platycheles</i> *	62	A				?	P	
<i>Ovalipes australiensis</i>	1				P			moribund
<i>Pachygrapsus laevimanus</i>	2		P					
<i>Paragrapsus laevis</i> *	8	P				F	P	
<i>Pilumnopus serratifrons</i>	11		P			P		
<i>Portunus pelagicus</i>	6				P			netted
<i>Sesarma erythrodactyla</i>	5			C			A	
<i>Thalamita intermedia</i>	1	P						in <i>Zostera</i>
<i>Thalamita sima</i> *	4				P			
<i>MOLLUSCA: POLYPLACOPHORA</i>								
<i>Ischnochiton elongatus</i>								
<i>crispus</i>	1				P			on stones
<i>BIVALVIA</i>								
<i>Ambuscintilla praemium</i> *	7	P						
<i>Anadara trapezia</i> *	21	P			C			
<i>Arthritica helmsi</i> *	57	A			P	A	F	
<i>Bankia cf. carinata</i>	2			C				in rotten logs
<i>Cyammimactra cf. symmetrica</i> *	2				P			
<i>Eumarcia fumigata</i> *	50	C				P	P	
<i>Fluviolanatus amarus</i> *	3	P					P	
<i>Glaucomomya plankta</i>	1						P	mangrove mud
<i>Irus crenata</i> *	1	P						
<i>Katelsia rhytiphora</i> *	6	P			P			in <i>Zostera</i> beds
<i>Katelsia scalarina</i>	1	P						
<i>Lasaea australis</i>	3		P				C	among <i>Galeolaria</i> tubes at mouth in weed beds
<i>Laternula creccina</i> *	11	P			P			
<i>Mesodesma elongata</i> *	8	P					P	
<i>Musculus cumingianus</i>	1		P					

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Species		Merimbula			Back Lake	Pambula estuary	Remarks	
	Nos. recorded	Intertidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal			
	1	2	3	4	5	6	7	8
<i>Mysella</i> sp.*	48	C			C		F	
<i>Mytilus edulis</i>	4		P		F		P	
<i>Notospisula trigonella</i> *	5	P			P			
<i>Ostrea angasi</i>	1		P					
<i>Psammobia donacioides</i> *	8	P			P	C		
<i>Saccostrea commercialis</i>	12		A			A-P*	A	+90% dead in March
<i>Solemya velesiana</i> *	2				P			
<i>Tapes</i> cf. <i>watlingi</i> *	1	P						
<i>Tellina</i> (<i>Abranda</i>) <i>hypelliptica</i>	1				P			
<i>Tellina</i> (<i>Abranda</i>) <i>modestina</i> *	1				P			
<i>Tellina</i> (<i>Macomona</i>) <i>deltoidalis</i> *	34	C			C	P	C	
<i>Trichomya hirsuta</i>	8		P		C			on rock or gravel
<i>Wallucina assimilis</i> *	23	C			C			
<i>Xenostrobus securis</i>	8		F			P	C	
GASTROPODA: PROSOBRANCHIA								
<i>Assimineia tasmanica</i>	2					P	F	in low salinity
<i>Austrocochlea constricta</i> *	38	P	C		F	F	P	
<i>Bedeva hanleyi</i> *	21	P			F			
<i>Bembicium auratum</i>	9		A			A	P	
<i>Bembicium melanostomum</i>	1		P					near mouth
<i>Bembicium nanum</i>	7		C	A		C	C	
<i>Bittium lacertinum</i> *	10	P			A			sea grass beds
<i>Patelloida mimula</i>	15		F			P	F	on oysters
<i>Cominella eburnea</i>	1		P					near mouth
<i>Diala</i> sp. * MER 51 J	18	F			A			on <i>Zostera</i>
<i>Hinea braziliana</i>	1						P	rock near mouth
<i>Hydrobia buccinoides</i>	3	P			A	A		low salinity
<i>Littorina scabra</i>	4			P			P	on mangroves
<i>Littorina unifasciata</i>	5		C				C	
<i>Melosidula zonata</i>	1						P	on mangroves
<i>Montfortula conoidea</i>	2		P					
<i>Morula marginalba</i>	2						P	rocks near mouth
<i>Nassarius burchardi</i> *	42	F			C	C	P	
<i>Nassarius jonassii</i> *	50	C			F	C	F	
<i>Nerita atramentosa</i>	8		F			F		
<i>Neritina</i> sp.* MER 283 K	2	P						sea grass beds
<i>Nodolittorina pyramidalis</i>	1		P					rock at mouth
<i>Patelloida alticostata</i>	1		P					
<i>Polinices</i> (<i>Conuber</i>) <i>sordidus</i> *	17	F					P	
<i>Prothalotia comtessei</i> *	18	P			F			on <i>Zostera</i>
<i>Pseudolittotia micans</i> *	10	F			P		P	on <i>Zostera</i>
<i>Pyrazus ebeninus</i> *	25	C				C	A	
<i>Tatea kesteveni</i>	4			P			A	in low salinity
<i>Tatea rufilabris</i>	1	P						
<i>Velacumantis australis</i> *	5	P				P	P	

Species	Merimbula					Back Lake	Pambula estuary	Remarks
	Nos. recorded	Intertidal sandy mud	Rocks and oyster racks	Salt marshes and mangroves	Subtidal			
	1	2	3	4	5	6	7	8
GASTROPODA: OPISTHOBRANCHIA								
<i>Akera soluta</i> *	15	F						
<i>Aplysia</i> cf. <i>dactylomela</i> (juv.)	1	P						
<i>Chemnitzia</i> sp. MER 220 M	1	P						
<i>Cingulina spina</i> *	13	P			F			
<i>Odostomia</i> sp. MER 219 X	1	P						
GASTROPODA: NUDIBRANCHIA								
" <i>Aclis</i> " MER 51 L, 58 P	2	P						in <i>Zostera</i>
GASTROPODA: PULMONATA								
<i>Ellisiphon</i> cf. <i>denticulatus</i>	3		P					
<i>Ophiocardelus quoyi</i>	8			F			P	
<i>Ophiocardelus sulcatus</i>	1						P	
<i>Onchidella patelloide</i>	2	P						
<i>Salinator fragilis</i> *	3	P						
<i>Salinator solida</i>	4			A		F	A	
<i>Siphonaria</i> cf. <i>diemenensis</i>	1		P					
CEPHALOPODA								
<i>Euprymna stenodactyla</i>	1				P			in <i>Zostera</i>
<i>Idiosepius notoides</i>	1				P			in <i>Zostera</i>
ECHINODERMATA								
<i>Patiriella exigua</i>	2		P					
<i>Amphipholis squamata</i>	3	P			P			
<i>Leptosynapta dolabrifera</i> *	10	P			P			
Synaptidae ?gen. MER 285 T	2				P			
CHORDATA: ASCIDIACEA								
	8		P					

NOTE: Nr. means close to this genus, may represent an undescribed genus.
 cf. means close to that species, but not that species, again may represent an
 undescribed species? Implies identification of genus or species is doubtful.

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TABLE 2. List of fish (Chordata: Pisces) recorded in Merimbula and Pambula estuaries.

Scientific and common name	Number of records	Merimbula	Pambula	and Remarks Total caught
<i>Acantholeuteres spilomelanurus</i> — leather jacket	3	P		9
<i>Acanthopagrus australis</i> — yellow fin bream	1	P		1
<i>Acanthopagrus butcheri</i> — black bream	1	P		4
<i>Aldrichetta forsteri</i> — yellow-eyed mullet	2	P		27
<i>Ammotretis rostratus</i> — flounder	5	P		13
<i>Arenigobius bifrenatus</i> — goby	2	P		2
<i>Argyrosomus hololepidotus</i> — mulloway	1	P		1
<i>Centropogon australis</i> — fortesque	7	F	P	16
<i>Chrysophrys auratus</i> — snapper	2	P		3
<i>Cheilinus bimaculatus</i> — wrasse	1	P		1
<i>Cristiceps australis</i> — crested weedfish	2	P		2
<i>Enoplosus armatus</i> — oldwife	1	P		2
<i>Favonigobius lateralis</i> — long finned goby	2	P		2
<i>Favonigobius tamarensis</i> — tamar river goby	3	P	P	5
<i>Girella tricuspidata</i> — blackfish	9	C	F	ca. 100
<i>Gobiopterus semivestitus</i> — transparent goby	1	P		1
<i>Hippocampus abdominalis</i> — seahorse	1	P		1
<i>Hyporhamphus australis</i> — garfish	2	P		7
<i>Lethrinus nematacanthus</i> — scavenger	1	P		1
<i>Meuschenia freycineti</i> — leather jacket	2	F		33
<i>Meuschenia hippocrepis</i> — variable leather jacket	2	P		2
<i>Meuschenia trachylepis</i> MER 105 E	4	P		5
<i>Monacanthus chinensis</i> — fan bellied leather jacket	1	P		1
<i>Mugil cephalus</i> — sea mullet	1	P		9
<i>Mugil georgii</i> — fantail mullet	1	P		1
<i>Mugilidae</i> (juveniles)	1	A		40
<i>Muraenichthys australis</i> — worm eel	1	P		1
<i>Myxus elongatus</i> — sand mullet	1	P		1
<i>Neoodax balteatus</i> — little rock whiting	1	P		2
<i>Nesogobius pulchellus</i> — pretty goby	5	C		75
<i>Nesogobius</i> sp. MER 278 T — goby	2	P		5
<i>Ophisurus serpens</i> (juv.) — snake eel	2	P		2
<i>Parkraemia ornata</i> — ornate goby	3	P		3
<i>Penicipelter vittiger</i> — leather jacket	1	P		1
<i>Petroscirtes lupus</i> — blenny	2	P		2
<i>Platycephalus fuscus</i> — dusky flathead	3	C		51
<i>Platycephalus laevigatus</i> — smooth flathead	1	P		1
<i>Platycephalus marmoratus</i> — marbled flathead	1	P		2
<i>Pomatomus saltatrix</i> — tailor	2	P		5
<i>Pranesus ogilbyi</i> — hardyhead	1	P		2
<i>Pseudogobius olorum</i> — swan river goby	1		P	1 low salinity
<i>Redigobius macrostoma</i> — large mouthed goby	3	P	P	7
<i>Rhabdosargus sarba</i> — tarwhine	2	P		3
<i>Scorpaena</i> cf. <i>cruenta</i> — rock cod	1	P		4
<i>Sillago ciliata</i> — sand whiting	4	F		16
<i>Sillago maculata</i> — trumpeter whiting	1	P		4
<i>Stethojulis interrupta</i> — wrasse	1	P		12
<i>Stigmatophora argus</i> — spotted pipefish	5	A		95
<i>Stigmatophora nigra</i> — pipefish	4	A	P	206
<i>Syngnathus phillipi</i> — pipefish	6	P	P	9
<i>Torquigener glaber</i> — puffer	3	P	P	5

Scientific and common name	Number of records	Merimbula	Pambula	Total caught and Remarks
<i>Torquigener hamiltoni</i> — puffer	3	P		3
<i>Urocampus carinirostris</i> — pipefish	6	P	P	12
<i>Usacaranx georgianus</i> — trevally	6	A		213
<i>Vincentia chrysurus</i> — cardinal fish	1	P		2

TABLE 3. Aquatic birds recorded by David Milledge (pers. comm.) in Eurobodalla Shire estuaries in 1974-76. Species seen at Merimbula marked with an asterisk. Relative abundance shown by R = rare; O = occasional; F = frequent; C = common; dotted line means present at that level throughout year.

Scientific and common name	Winter	Spring	Summer	Autumn	Habits	Food
<i>Anas castanea</i> — chestnut tealF.....				dabbler	invertebrates
<i>Anas gibberifrons</i> — grey tealO.....				dabbler	invertebrates
<i>Anas superciliosa</i> * — black duckF.....				dabbler	invertebrates and algae
<i>Ardea novaehollandiae</i> * — white-faced heronC.....				wader	fish and crustacea
<i>Arenaria interpres</i> — turnstone			R		wader on mud, sand and rocks	invertebrates
<i>Butorides striatus</i> — mangrove heronF.....				wader in mangroves and on oyster racks	crustacea
<i>Calidris acuminata</i> — sharp tailed sandpiper			R		wader on sandy mud	invertebrates
<i>Calidris canutus</i> — knot		O	F		wader on sandy mud	invertebrates
<i>Calidris tenuirostris</i> — great knot			R		wader on sandy mud	invertebrates
<i>Calidris ferruginea</i> * — curlew sandpiper			R		wader on sandy mud	invertebrates
<i>Calidris ruficollis</i> — red-necked stint		O	O		wader on sandy mud	invertebrates
<i>Charadrius bicinctus</i> — double banded dotterel	F			F	wader on muddy sand	invertebrates
<i>Charadrius mongolus</i> — Mongolian dotterel			R		wader on muddy sand	invertebrates
<i>Charadrius ruficapillus</i> — red-capped dotterelF.....				wader on muddy sand	invertebrates
<i>Cygnus atratus</i> * — black swanC.....				swimmer	grazes on <i>Zostera</i> etc.
<i>Egretta alba</i> — white egretF.....				wader	fish and crustacea
<i>Egretta garzetta</i> * — little egretF.....				wader	fish and crustacea
<i>Egretta sacra</i> — reef heronO.....				wader on rocky shores	fish and crustacea

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Species and common name	Winter	Spring	Summer	Autumn	Habits	Food
<i>Haematopus fuliginosus</i> * — sooty oystercatcher	F			wader on rocks and oyster racks	invertebrates
<i>Haematopus longirostris</i> * — pied oystercatcher	C			wader on sandy mud	mainly crustacea
<i>Hydroprogne caspia</i> — caspian tern			R		plunge dives	fish
<i>Larus novaehollandiae</i> * — silver gull	C			scavenges on shores and shallows	general carnivore
<i>Limosa lapponica</i> * — bar-tailed godwit		C	C		wader on mud	mainly polychaetes
<i>Numenius madagascariensis</i> * — eastern curlew		C	C		wader on mud in mangroves	invertebrates
<i>Numenius phaeopus</i> — whimbrel		O	O		wader on mud, sand and stones	invertebrates
<i>Pelecanus conspicillatus</i> — Australian pelican			O		swimmer	fish
<i>Phalacrocorax carbo</i> * — black cormorant	C			swimmer and diver	fish
<i>Phalacrocorax melanoleucos</i> * — little pied cormorant	C			swimmer and diver	fish
<i>Phalacrocorax sulcirostris</i> * — little black cormorant	O			swimmer and diver	
<i>Platalea regia</i> — royal spoonbill	O			wader in shallows	invertebrates
<i>Pluvialis dominica</i> — eastern golden plover	R			wader on sandy mud	invertebrates
<i>Pluvialis squatarola</i> — grey plover	R			wader on sandy mud	invertebrates
<i>Podiceps poliocephalus</i> — hoary-headed grebe	R			swimmer	fish and weed
<i>Sterna albifrons</i> — little tern	O			plunge dives	fish
<i>Sterna bergii</i> * — crested tern	C			plunge dives	fish
<i>Sterna hirundo</i> — common tern			R		plunge dives and dips	fish
<i>Threskiornis aethiopica</i> — white ibis	O ...	R		wader on mud flats	invertebrates
<i>Tringa hypoleucos</i> — common sandpiper		O			wader on sandy mud and rock	invertebrates
<i>Tringa nebularia</i> — greenshank			R		wader on muddy sand	invertebrates
<i>Vanellus miles</i> — spur-winged plover	F			wader on rocks and mulflats	invertebrates

DISCUSSION

This survey of Merimbula Lake and the nearby estuaries provides some basic data on the animals and the plants occurring there. The resultant species list (Table 1) can be compared with other estuarine areas in New South Wales, although as mentioned in the Introduction, faunal and floral surveys of New South Wales

estuaries are few and even when they have been carried out, some taxonomic problems exist, for example polychaetes which were almost all identified to species at Merimbula have often not been identified elsewhere. Thus some caution must be taken in interpreting and comparing species lists. Many species occurring in estuaries are not consistently present and, unless regular sampling is carried out, will appear absent.

Recently Hutchings and Murray (in press) have described the polychaete fauna of New South Wales estuaries (over 180 species). They found that Merimbula shares some species in common with more northerly regions but some species have only been reported from Merimbula. Although the Australian Museum has extensive polychaete collections from New South Wales, many areas have been poorly collected especially the northern rivers and so it is premature to comment on the zoogeography of estuarine polychaetes in the state or along the east coast of Australia. Many more species, including many undescribed ones will probably be found to occur in the region. Similar problems arise with the crustaceans, and many of the dominant isopods and amphipods found at Merimbula have not been fully identified. The decapods collected from Merimbula share many species in common with Sydney areas (Hutchings and Recher, 1974). Molluscs are probably the best known group of estuarine invertebrates, and for this group an area just further south at Green Cape (Rudman, pers. comm.) represents an important transition zone between southern and northern faunas. Merimbula has a similar mollusc fauna to those areas further north in New South Wales.

In summary it is premature to compare in detail the estuarine fauna and flora of Merimbula with other estuarine areas of New South Wales, however some general comments can be made. Lake Merimbula has a rich and diverse estuarine fauna which shares many species in common with areas further north in New South Wales, but the fauna also has a southern component. However, detailed information on estuarine fauna further south is almost completely lacking except for the molluscs.

Although information on salinity and sediment was collected at Merimbula it was not collected systematically enough to correlate the fauna with these two physical parameters in any detailed way except perhaps on the three line transects carried out in Merimbula Lake which will be dealt with in a subsequent paper. However, in general polychaetes, one of the dominant infaunal groups do not necessarily show a good correlation with sediment type (Jones, in press) and although sediment must be important other factors such as salinity have an overriding effect. Some polychaetes however do show a specific sediment relationship in the Hawkesbury (Jones, pers. comm.). Collett *et al.* (in press) have analysed the infauna of *Posidonia* seagrass beds and have shown that the fauna in Top Lake is different from East Lake, presumably due to differences in salinity. The *Posidonia* fauna of East Lake showed more similarity with estuarine sites further north, than with the fauna of Top Lake, suggesting that latitudinal differences may be less important than salinity.

The polychaete fauna of Merimbula resembles many other estuarine areas in that a species may occur in a wide variety of estuarine habitats, including intertidal, subtidal, bare muddy substrates and seagrass beds (both *Posidonia* and *Zostera*). Although in Table 1, subtidal habitats are not classified, Hutchings and Recher (1974) gave lists of species which occur in both seagrass habitats, which appear to be very different physical habitat. Hutchings and Recher (1982) have postulated that in temperate areas, the mangrove fauna is basically the fauna of adjacent intertidal mud flats whereas in the sub-tropics and tropics a specialised mangrove fauna occurs which does not overlap with the fauna of adjacent mud flats. The mangrove fauna at Merimbula supports this hypothesis.

We believe that our study of Merimbula has provided a framework on which a more detailed study can be planned, and hypotheses generated and tested on the factors important in determining the distribution of estuarine animals. Only then can valid comparisons be made between similar estuaries; for along the New South Wales coast a wide variety of estuaries and lagoons occur which can be relatively easily characterised by their geomorphology, flushing patterns, fresh water inputs (Chapman *et al.*, 1982; Roy, 1982). Superimposed upon these physical characteristics are varying levels of man's impact on the estuary, which are difficult to determine, but which must be determined, if valid comparisons of estuarine fauna's and flora's are to be made. However it seems likely that although some broad generalisations can be made about similar physical estuaries, each estuary has its own unique characteristics.

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The complete larval development, under laboratory conditions, of *Heteropanope glabra* Stimpson 1858 (Brachyura, Xanthidae), from Australia

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ABSTRACT

Larvae of *Heteropanope glabra* reared in seawater of 35‰ salinity at 25°C temperature passed through four zoea stages to the megalopa in 10 days. The zoeal and megalopal stages are figured and described. The first zoea is unlike that previously described for this species by Aikawa (1929), confirming a previous suspicion that Aikawa's material was misidentified. This necessitates a reappraisal of features differentiating *Heteropanope* from *Pilumnopus*, and the position of these two genera within the Xanthidae. These matters are discussed.

INTRODUCTION

Heteropanope glabra Stimpson is a widely distributed small crab occurring from eastern Australia northwards to Japan and westwards through Indo-Malaysia to Zanzibar (Balss, 1933).

As noted elsewhere by the authors (Greenwood and Fielder, in press) no larvae are known for species of this genus. Accepting the generic distinctness of *Pilumnopus* (*sensu* Takeda and Miyake, 1969), the only larva attributed to a species of *Heteropanope* is that mistakenly ascribed to *Heteropanope glabra* by Aikawa (1929). It is evident (see this paper and Takeda and Miyake, 1968) that Aikawa misidentified the parentage of his larvae, which probably belonged to *Pilumnopus indicus* (de Man).

The present paper describes the four zoeal stages and megalopa of *H. glabra*, and is one of a series describing larval development of crabs occurring in central eastern Australia.

METHODS

Ovigerous females (carapace width 15-19 mm, \bar{x} 15.75 mm) were collected from lower intertidal habitats near the mouth of the Brisbane River, Queensland (Lat. 27°23'S; Long. 153°9'E). In the laboratory, captured crabs were maintained

in pasteurised seawater of 34‰ salinity in plastic containers (160 x 160 mm) with a water depth of 50 mm. A small piece of nylon gauze was provided as a substrate for each crab. All containers were kept at 25°C with a 12/12 hour light/dark cycle. Water in all containers was changed daily. Hatched zoeae were transferred in batches of 1-200 into separate similar containers and newly hatched *Artemia* nauplii added as food. Water and food were changed daily.

TABLE 1. Dimensions of zoeae of *Heteropanope glabra*. (In mm; mean of 10 individuals per zoeal stage, standard deviation in brackets).

FEATURE	ZOEAL STAGE			
	1	2	3	4
Carapace (A)	0.54(0.03)	0.62(0.03)	0.74(0.05)	0.94(0.04)
Range	0.48-0.6	0.6-0.7	0.68-0.8	0.88-0.98
Dorsal Spine (B)	0.76(0.09)	0.84(0.05)	0.8(0.2)	1.17(0.12)
Range	0.5-8.2	0.8-0.9	0.58-1.0	1.0-1.36
Rostrum (C)	0.59(0.04)	0.71(0.09)	0.79(0.1)	1.02(0.07)
Range	0.54-0.62	0.6-0.9	0.66-1.0	0.88-1.12
2nd Antenna (D)	0.4(0.02)	0.4(0.02)	0.43(0.03)	0.55(0.04)
Range	0.36-0.44	0.36-0.42	0.38-0.48	0.46-0.6
Spine to Rostrum (E)	1.67(0.1)	1.86(0.14)	2.2(0.3)	2.79(0.1)
Range	1.4-1.74	1.82-1.9	1.78-2.4	2.62-2.88
Lateral spines (F)	0.89(0.05)	1.02(0.05)	1.28(0.07)	1.6(0.11)
Range	0.8-0.96	0.96-1.04	1.16-1.36	1.3-1.78
Ratio B/A	1.4	1.3	1.1	1.2
Ratio B/C	1.3	1.2	1.0	1.1
Ratio D/C	0.7	0.6	0.5	0.5

Methods used in examining, dissecting and drawing larvae were similar to those previously used by the authors (e.g. Greenwood and Fielder, 1979). Measurements of larvae were made with the aid of a micrometer eyepiece and are given in tabular form (Table 1). In zoeae: spine to rostrum length is the direct distance between the extremities of the dorsal spine and rostrum; rostrum and antennal lengths from their distal tips to the anterior border of the orbit; dorsal spine length, from its tip to the centre of its axis at a point in profile with the carapace; lateral spine width (Table 1, F) as the maximum distance between the tips of the lateral carapace spines; carapace length, from the anterior border of the orbit to the postero-medial cleft of the carapace. Megalopa carapace length was measured from the tip of the rostrum to the postero-medial carapace border; carapace width was measured at the widest point.

Details of setation were determined using phase-contrast microscopy, and in some cases use of chlorazol black or lignin pink staining. Appendage structure

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is figured, and details of setation are given in tabular form (Tables 2 and 3). To reduce repetition, detail of all appendages is figured for only the first, third and final zoeal stages, and the megalopa. Figures for zoeal stage 2 are available from the authors upon request.

RESULTS

Four zoeal stages occur prior to the moult to the megalopa. Development time through these stages was 10 days. All zoeae were released within two minutes of the first hatching. Dimensions of zoeae are given in Table 1, and details of setation of zoeal and megalopal stages in Tables 2 and 3 respectively.

Zoea 1 (Figs. 1 A, B; 2 A-G; Tables 1, 2)

TABLE 2. Setation details of zoeal appendages of *Heteropanope glabra*. (A = aesthete, S = simple seta, SP = sparsely plumose, P = plumose, HP = highly plumose, PD = plumodenticulate).

Appendage	ZOEAL STAGE			
	1	2	3	4
Antenna 1				
Terminal	3A, 2S	5A, 2S	4A, 2S	4A, 2S
Subterminal	0	0	1A	7A
Antenna 2				
Exopod	10-20spines, 2S	10-20spines, 2S	13-16spines, 2S	8-18spines, 2S
Peduncle process	14-20spines	12-20spines	12-20spines	9-10spines
Endopod	absent	small	c.0.3 x exop.	c.0.5 x exop.
Maxilla 1				
Coxa	0	1HP, 1PD	1HP, 1PD	1HP, 1PD
Coxal endite	8PD	7PD	7PD	7-8PD
Basal endite	2SP, 3PD	5SP, 4PD	5SP, 4PD	5SP, 5-6PD
Endop. seg. prox.	1PD	1PD	1PD	1PD
seg. 2	4+2PD	4+2PD	6PD	6PD
Maxilla 2				
Coxal endite, prox.	6PD	6PD	6PD	6PD
dist.	4PD	4PD	4PD	4PD
Basal endite, prox.	3PD, 2S	3PD, 2S	3PD, 2S	5PD, 1S
dist.	3PD, 1S	4PD, 1S	6PD	5-6PD
Endop. prox. lobe	3PD	3PD	3PD	3PD
dist. lobe	4PD, 1S	4PD, 1S	5PD	5PD
Scaphognathite	4+1HP	11HP	18-19HP	c.26HP
Maxilliped 1				
Basis	9PD, 2S	8PD, 2S	10-11PD	8PD, 2S
Endop. seg. prox.	2PD, 1S	1PD, 2S	1PD, 2S	1PD, 2S
2	1PD, 1S	1PD, 1S	1PD, 1S	1PD, 1S
3	1PD	1PD	1PD	1PD
4	1PD	2PD	2PD	2PD
5	4PD, 1S	4PD, 1S	4PD, 2S	5PD, 1S
Exopod	4HP	6HP	8HP	10HP
Maxilliped 2				
Basis	4PD	4PD	4PD	4PD
Endop. seg. prox.	1PD	1PD	1PD	1PD
2	1PD	1PD	1PD	1PD
3	2PD, 4S	3PD, 3S	3PD, 3S	5PD, 1S
Exopod	4HP	6HP	8HP	10HP

Eyes immobile. All carapace spines well developed and prominent; dorsal spine straight and very long, almost one-half longer than carapace and one-third longer than rostrum; lateral spines conspicuous, directed laterally to acute point, each c. 0.2 mm long, distance between tips greater than length of dorsal spine; rostrum smooth, straight, two-thirds length of dorsal spine, of similar length to carapace. Antennal spinous process two-thirds length of rostrum. Abdomen with five somites; second and third with mid-lateral processes as figured; small rounded postero-lateral processes on somites 3-5 all of similar size; somites 2-5 each with a postero-dorsal prominence bearing 2 small setules. Telson (Fig. 1 B, 2 G) with 3 + 3 biplumose inner setae lateral to acute median notch. Three outer telson spines (TOS), all arising well posterior to the bases of the inner setae; TOS 1 and 3 arise dorsally and do not overlap; TOS 3 is the longer and situated near constriction at base of cornua; TOS 2 minute and hair-like arises laterally at constriction.

Zoea 2 (Fig. 1 C; Tables 1, 2)

Eyes now mobile. Carapace larger, more globose than previously, dorsal spine slightly shorter and rostral spine slightly longer. Lateral carapace spines large and now with slight ventral curvature. Small buds of posterior thoracic limbs present. Sixth abdominal somite still fused to telson; postero-lateral processes of somites 3-5 still of similar length, rounded, overlapping next somite by approximately one-quarter length. TOS 1 greatly reduced in size, telson otherwise little changed. *Zoea 3* (Figs. 1 D, E; 3 A-G; Tables 1, 2)

Carapace larger than in stage 2; change in proportions of spines similar to previous stage; dorsal spine now with slight posterior curvature, lateral spines now with slight postero-ventral curve. Thoracic limb-buds greatly enlarged, as long as bases of maxillipeds; chela distinct. Sixth abdominal somite now distinct from telson, other somites as previously, but slight ventral swelling in presumptive pleopod region. Telson with additional small biplumose seta on either side of postero-medial cleft giving formula 4 + 4; otherwise little changed.

Zoea 4 (Figs. 1 F, 4 A-G; Tables 1, 2)

Continued size increase and change in proportions of carapace processes. Abdominal somites 2-6 now with well developed elongate pleopod buds, those on somite 6 being smallest; postero-lateral processes on somites 3-5 now acutely pointed and overlap next somite by approximately one-third length. Telson as previously.

Megalopa (Figs. 5 A-G, 6 A-I; Table 3)

Dimensions (mean of 5 measurements): carapace length 0.99 mm (tip of rostrum to postero-medial border); carapace width 0.95 mm.

Carapace broad posteriorly with margins fringed by setules, narrowing anteriorly to inter-orbital rostral plate. Rostral plate broad, almost half width of carapace; lateral borders almost parallel; anterior border approximately trilobed, having a median rounded and slightly downcurved rostral lobe, and a pair of more acute anteriorly directed lateral lobes.

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Abdominal somites 2-5 with each postero-lateral border curved sinusoidally and produced ventro-laterally into a posteriorly directed acute process overlapping following somite; processes of fifth somite longest, overlapping most of sixth. All somites with dorsal and dorso-lateral setules, formula (somites 1-6) 12,8,10,12,14,4. Telson almost semicircular, two setules subterminally on dorsal surface, four on ventral.

Appendage details as figured and tabulated. All pereopods fully developed, notably each with ventral or postero-ventrally directed stout thorn-like spines on proximal segments: pereopods 2-5 each have one such spine on the ischium; pereopod 1 has three on the ischium, also three similar spines on the merus subventrally.

Pleopods fully developed on abdominal somites 2-5, first pair approximately 1.5 x length of last. Exopods fringed with 10-12 long biplumose setae; endopods small, with three minute hooked setae disto-medially. Uropods uniramous, two-segmented; proximal segment with single lateral biplumose seta, distal segment with six such setae peripherally.

TABLE 3. Setation details of megalopa appendages of *Heteropanope glabra*. (Abbreviations as in Table 2).

Appendage	Setation	Appendage	Setation
Ant. 1 peduncle	2-3S	Max'ped 1 Coxal end.	8-10PD
inner flag.	5PD, 1S	basal end.	9-11PD
term. flag.	0	endopod	4S
seg. 2	8A	exop. seg. 1	2HP
3	6A, 3S	2	5HP
4	4A, 2S	epipod	7-8PD
Ant. 2 flagellum		Max'ped 2 basis	2PD
seg. 1	2S	endop. seg. 1	1PD, 1-2S
2	1S	2	1PD
3	1S	3	4-5PD
4	0	4	4SP, 2PD, 1S
5	0	exop. seg. 1	1PD
6	0	2	5HP
7	5S	epipod	small
8	0	Max'ped 3 basis	14-17PD, 2S
9	3S	endop. seg. 1	8-10PD, 5S
10	4S	2	5PD, 4-5S
Max. 1 coxal end.	11-13PD	3	2PD, 3S
basal end.	11PD, 6SP	4	6PD, 4S
endop. seg. 1	1PD	5	5PD, 2S
2	1PD	exop. seg. 1	1S
3	1PD, 2S	2	4HP, 2S
coxa	2PD, 1HP	epipod.	9-12PD
Max. 2 coxa prox. end.	7-8PD		
dist. end.	4PD		
basis prox. end.	4-5PD		
dist. end.	6PD, 3S		
endopod	1HP, 2S		
scaphognath.	45HP, 3S		

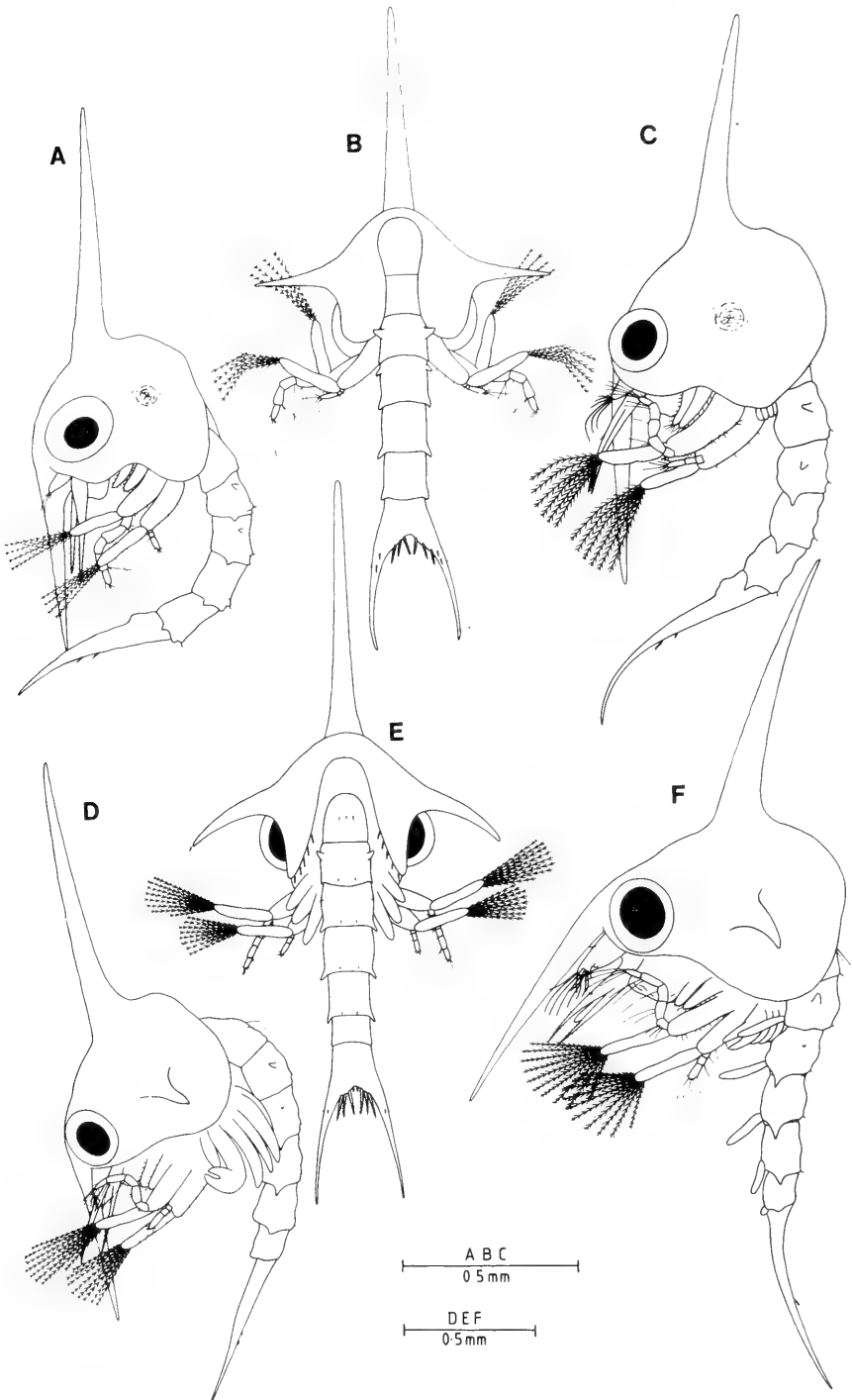


Fig. 1. *H. glabra* zoeal stages. A, first zoea lateral view; B, first zoea posterior view; C, second zoea lateral view; D, third zoea lateral view; E, third zoea posterior view; F, fourth zoea lateral view.

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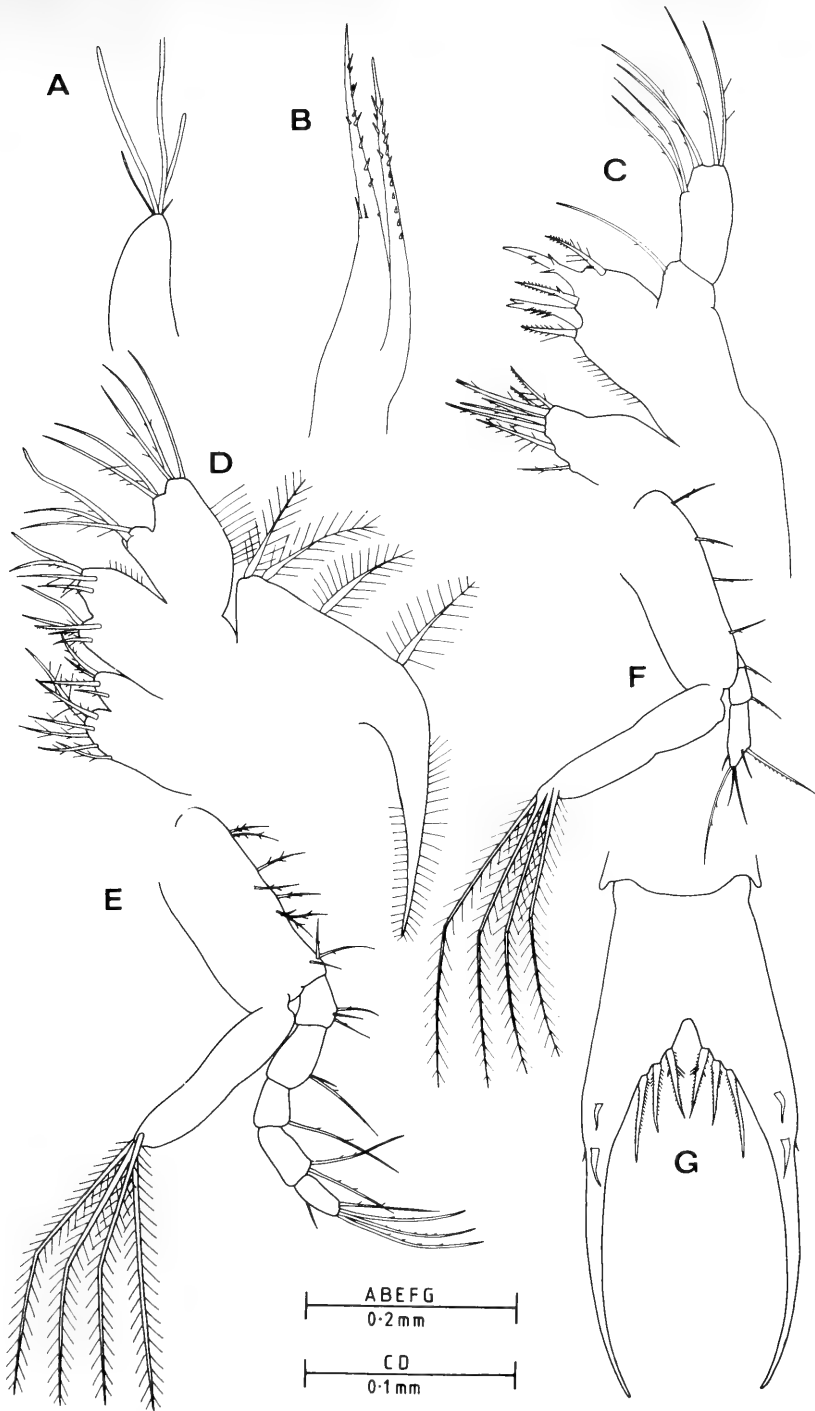


Fig. 2. *H. glabra* first zoea's appendages. A, first antenna; B, second antenna; C, first maxilla; D, second maxilla; E, first maxilliped; F, second maxilliped; G, telson.

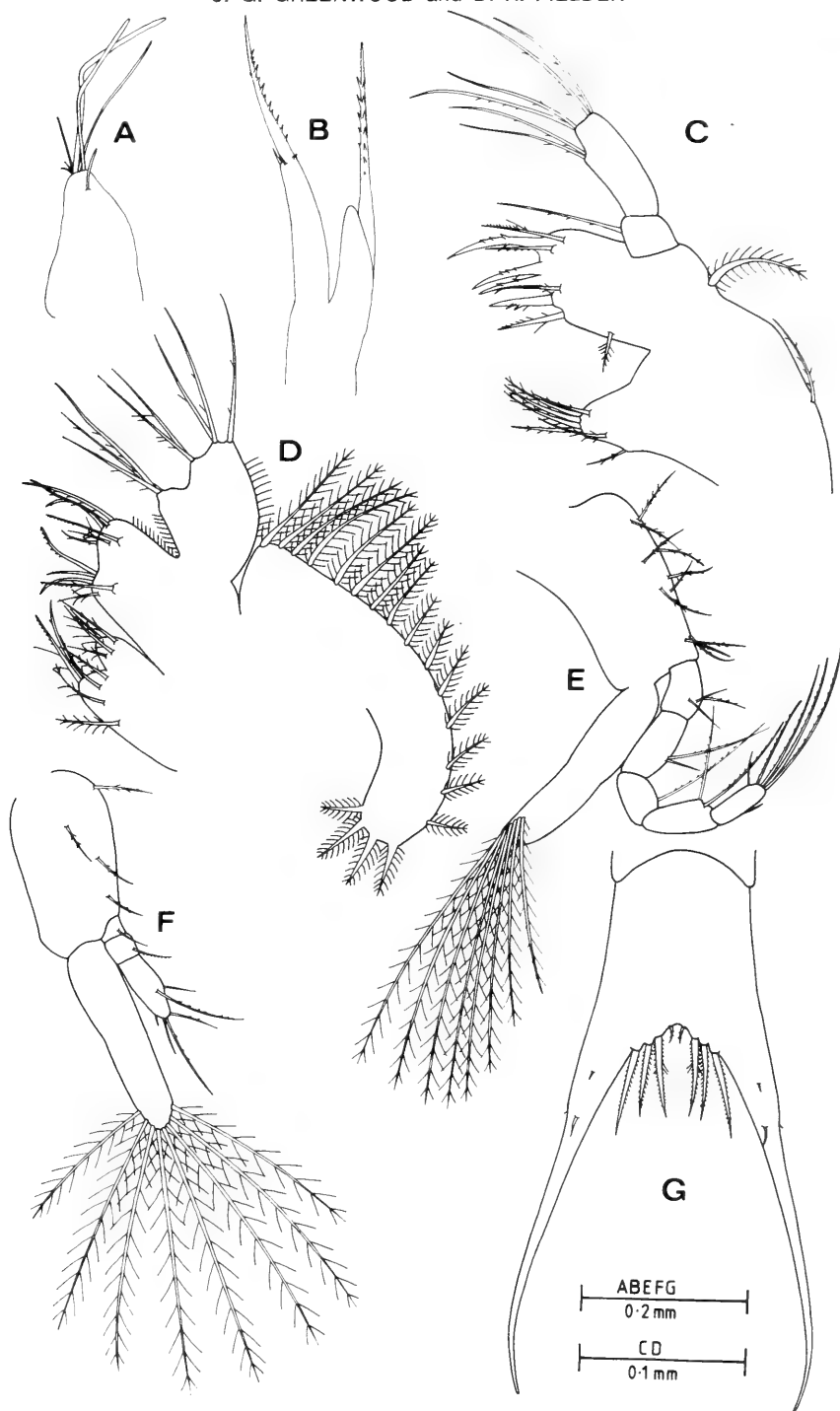


Fig. 3. *H. glabra* third zoea's appendages. A, first antenna; B, second antenna; C, first maxilla; D, second maxilla; E, first maxilliped; F, second maxilliped; G, telson.

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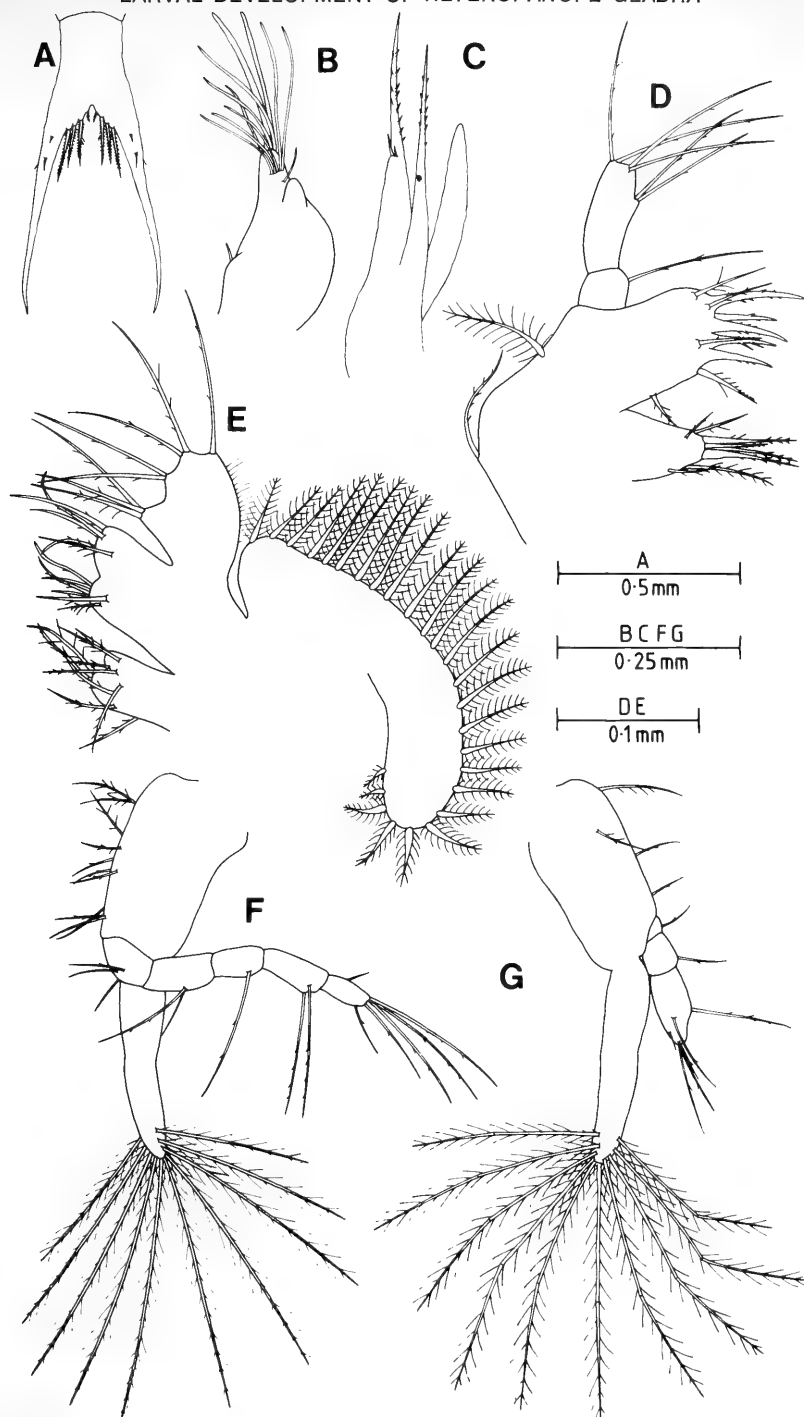


Fig. 4. *H. glabra* fourth zoea's appendages. A, telson; B, first antenna; C, second antenna; D, first maxilla; E, second maxilla; F, first maxilliped; G, second maxilliped.

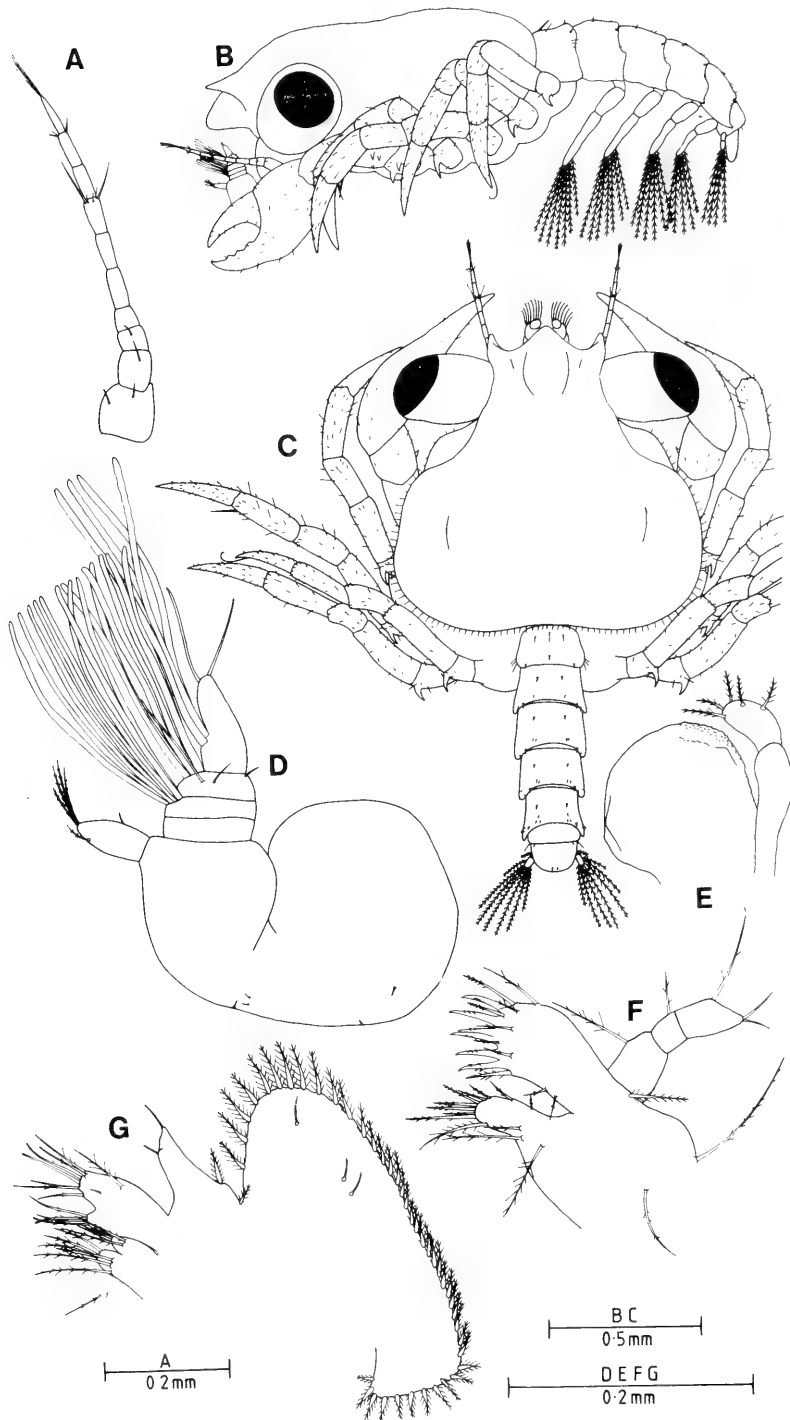


Fig. 5. *H. glabra* megalopa. A, second antenna; B, lateral view; C, dorsal view; D, first antenna; E, mandible; F, first maxilla; G, second maxilla.

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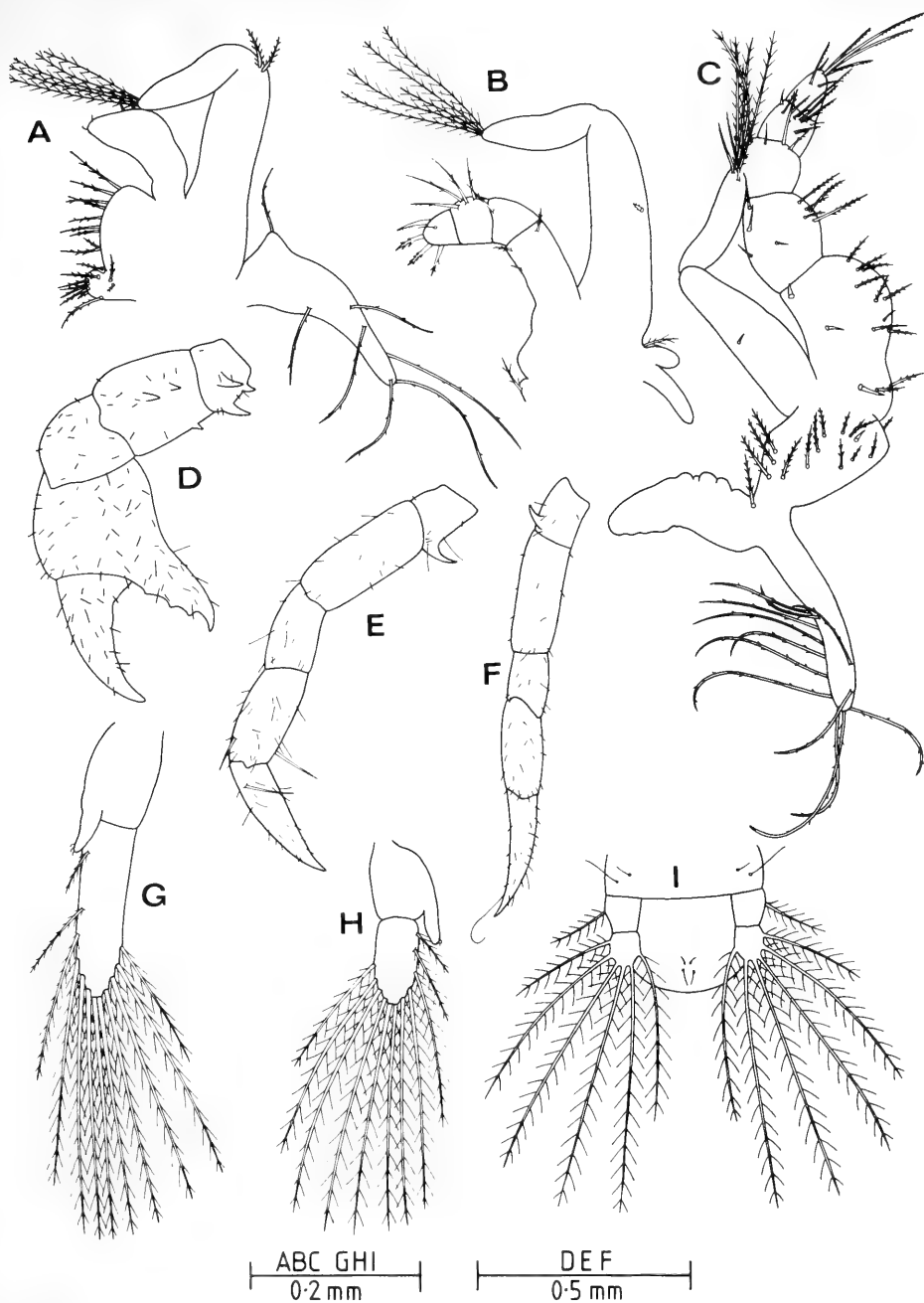


Fig. 6. *H. glabra* megalopa. A, first maxilliped; B, second maxilliped; C, third maxilliped; D, first pereopod; E, second pereopod; F, fifth pereopod; G, first pleopod; H, fourth pleopod; I, telson and uropods, ventral view.

DISCUSSION

There are obvious and major differences between the zoeae of *H. glabra* described here and the first zoeae attributed to that species by Aikawa (1929). Aikawa's zoeae contrast markedly with the present material in having: no rostral or lateral carapace spines (c.f. both present and well developed); a *curved* dorsal spine (possibly an artefact, but c.f. straight and rigid) whose length is only 0.64 x carapace length (c.f. 1.4 x); dorsolateral projections on only the second abdominal somite (c.f. on second and third somites); differences in details of setation, especially of the first maxilliped and endopod of the second maxilliped; absence of an apical process (*sensu* Dover *et al.*, type 7) on the scaphognathite (c.f. present).

The present findings confirm that Aikawa's (1.c.) zoeae were not of *H. glabra*. Indirect support is therefore given to the suggestion by Takeda & Miyake (1968), based on comparison with their larval material and distribution of adults, that Aikawa's (1.c.) zoeae may belong to *Pilumnopus indicus*.

The zoeal stages of *H. glabra* exhibit all those features suggested by Rice (1980) as typifying pilumnid xanthids, with the minor exception that the basis of maxilliped I here has 11 setae rather than the more usual 10. Some reappraisal of larval features distinguishing the genera *Pilumnopus* and *Heteropanope* is however necessary, for existing reviews of such features (e.g. Wear, 1970:86; Rice 1980:325,327) are based on knowledge of three species, two of whose generic status is now reversed. Thus all previous data on *Heteropanope* were derived from a probable *Pilumnopus* sp. closely resembling *P. indicus* (see above); similarly previous data on *Pilumnopus*, although derived in part from *P. indicus*, were also derived from *Heteropanope serratifrons* (see Greenwood & Fielder, in press).

Generalisations on these two genera and their position in the Xanthidae (e.g. Wear, 1970:86; Rice, 1980:327) must now be restated on the basis of data presently available for zoeae of *H. glabra* (present description), *P. indicus* (?Aikawa, 1929; Takeda & Miyake, 1968) and *P. serratifrons* (Wear, 1968; Greenwood & Fielder, in press). *H. glabra*, like most other pilumnids, has dorso-lateral knobs on both the second and third abdominal somites, whereas in *Pilumnopus* this feature is variable, there being such knobs on both (*P. serratifrons*) or only the first (*P. indicus*) of these somites. It can no longer be said the rostrum is "reduced or absent" in these genera, for whilst there is no evident rostrum in *P. indicus*, and it is very reduced in first zoeae of *P. serratifrons*, a rostrum is visible in later stages of *P. serratifrons* (though always much shorter than the antennal processes) and in *H. glabra* it is large in all stages, as in xanthids. Lateral carapace spines are present and large in *H. glabra*, whereas in *Pilumnopus* they may be absent (*P. indicus*) or present though relatively small (*P. serratifrons*); similar intragenetic variability in development of these carapace spines has been noted by the authors in zoeae of the soldier-crab genus *Mictyris*. As noted elsewhere (Greenwood & Fielder, in press), Wear's (1970) suggestion that these

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two genera should be recognised as forming a distinct group within the xanthids, because of their lack of rostral and lateral carapace spines, is no longer valid.

ACKNOWLEDGEMENTS

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The congress will be organized to include a wide range of topics, to appeal to all persons interested in the scientific study of amphibians and reptiles. The committee currently is setting guidelines for operations, including the establishment of a larger and broadly representative International Herpetological Committee to provide a self-perpetuating mechanism for future congresses.

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NOTICE TO AUTHORS

Papers will be considered for publication in *The Australian Zoologist* if they make an original contribution to whole animal biology of the Australian fauna. Papers submitted will be subjected to review and thence to the normal editorial process, in the course of which authors will receive edited galley proofs for correction. A manuscript is accepted on the understanding that it is to be published exclusively in *The Australian Zoologist*.

MANUSCRIPTS (original and two copies) should be sent to Dr. L. C. Llewellyn, the Editor, "The Australian Zoologist", National Parks and Wildlife Service (189 Kent Street), Box N189 Grosvenor Street P.O., Sydney, N.S.W. 2001. They should be typewritten (double spaced) on good quality paper. All pages of the manuscript must be numbered consecutively, including those containing references tables and figure legends, which should all be placed after the text. (Poor quality photocopies will not be accepted).

On the first page of the manuscript should appear the title of the paper, name of the author, the name of the Institution where the work was done and the present postal address if different from that of the Institution. Titles should be as brief, but as informative, as possible. A short title, to serve as a running heading and consisting of not more than 50 letters (including spaces) must also be given on the title page.

The abstract (up to 200 words) should state concisely the scope of the work and the principal findings and should be suitable for direct use by abstracting journals. The section headings should be Introduction, Materials and Methods, Results, Discussion, Acknowledgements and References. Presentation must be clear and concise and all unnecessary repetition especially in consecutive sections should be avoided. Footnotes should be avoided.

REFERENCES are cited in the text by the author and date and are not numbered. Authors are referred to the most recent issues of *The Australian Zoologist* for the style used. No editorial responsibility can be taken for the accuracy of the references; authors are requested to check these with special care. Abbreviations of titles of periodicals should conform to those used in *World List of Scientific Periodicals*, 4th Edition.

TABLES should be numbered with arabic numerals, be accompanied by a title and be typed on separate sheets. Their approximate position in the text should be indicated by a note in the margin.

ILLUSTRATIONS AND DIAGRAMS should be larger than the size of the finished block. Drawings must not exceed 30 x 20 cm. If the originals exceed this they should be photographically reduced and good quality prints provided. Half tone prints should be arranged as plates and mounted on stiff white board up to a maximum size of 30 x 20 cm. Authors will be allowed up to two plates free of charge, but will be expected to pay the cost of any additional plates.

SHORT PAPERS these should be no more than six typewritten pages long and should deal with a technique experiment or important observation not reaching lengthy treatment. Isolated factual notes would not be considered suitable.

EDITORIAL

This issue of 'The Australian Zoologist' is a composite. Part 4 consists of papers on vertebrate palaeontology that were submitted as a block. They arose from a symposium on 'The Cainozoic Evolution of Continental Southeast Australia' held at the Australian National University, Canberra, in November 1980. That symposium included some 54 papers, abstracts of which can be found in Record 1980/67 of the Bureau of Mineral Resources, Geology and Geophysics (Canberra 2600, Australia).

Papers submitted in the usual course of events comprise part 5. Clearly, without the unusual submission of the palaeontological papers that comprise part 4, there would not have been enough material for the journal to be printed at this time. It would have been well into 1985 before the issue covered by 1984 subscriptions could have been printed. For this and other reasons the council of the Royal Zoological Society of NSW has decided that 'The Australian Zoologist' in its present form as an irregular research journal is no longer viable. When the journal was first published in 1914 it filled an important gap. Over the years the fortunes of the journal have varied. At times it was a *de facto* specialist journal, usually reflecting the area of interest of the editor. In later years the role originally taken by 'The Australian Zoologist' has been ably filled by CSIRO sponsored journals such as 'Australian Journal of Zoology', 'Australian Journal of Biological Sciences' and 'Australian Wildlife Research'. Various specialist journals, such as 'Australian Mammalogy' have also appeared in recent years.

The council of the Royal Zoological Society of NSW has decided, in consultation with the various sections of the Society and with the broader community of Australian zoologists, that the publications policy of the Society should shift to meet current needs in Australian scientific publishing. As part of that shift, the next issue, 21(6/7), due in May 1985, will be the last issue of 'The Australian Zoologist' in its present format. Commencing with 22(1) in Sept. 1985 'The Australian Zoologist' will be a regular, quarterly publication. Each volume will consist of four parts: Sept. (1), Dec. (2), Mar. (3) and June (4). In this new format the journal will continue to include original scientific research papers, but they will be requested to be written in a manner readily understood and of interest to general zoologists. The new format journal will provide rapid publication of survey results and faunal lists. Short notes will be welcomed, as well as short review articles of general interest. The current quarterly magazine 'Kooilewong' will cease publication as of July 1985 and items of Royal Zoological Society business and information contained therein will be incorporated into 'The Australian Zoologist'.

Within the range of current Australian scientific publications there is no specific journal for scientific review articles. There are several publications for popular reviews, but nothing similar to 'Biological Reviews' or various annual review publications of the Northern hemisphere. Therefore the council of the Royal Zoological Society of NSW has resolved to publish an annual journal, 'Australian Zoological Reviews', beginning in 1985. This journal will be available as a separate subscription or in addition to subscriptions to 'The Australian Zoologist'. Further details can be obtained from the Secretary of the Royal Zoological Society (P.O. Box 20, Mosman NSW 2088, Australia).

M. L. Augee,
Editor.



The Fossil Vertebrate Deposits of Victoria Fossil Cave Naracoorte: An Introduction to the Geology and Fauna

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ABSTRACT

Victoria Fossil Cave, Naracoorte, southeastern South Australia is one of many caves in the Oligo/Miocene limestones of the Murray Basin. In late Pleistocene times it acted as a natural pitfall accumulating large numbers of vertebrates. The fauna from an excavation in the top 1.5m of the 4m deep deposit includes 78 taxa of which 17 are extinct and 14 have disappeared from the region in historic time. The bones of extinct browsing marsupials and associated predators are the most distinctive elements in the deposit, although for numbers of individuals the small rodents, marsupials, birds and reptiles predominate. The sequence of accumulation of sediments and bone suggests a change from a more mesic forest environment to a more xeric woodland in late Pleistocene times. Problems in interpreting stratigraphic succession and dating the deposit are discussed.

INTRODUCTION

Victoria Fossil Cave at Naracoorte in the southeast of South Australia contains arguably the largest accumulation of Pleistocene fossil vertebrates yet found at any cave site within Australia.

In this paper an interpretation is given of the geological history of the caves. A model is advanced to explain the mode and sequence of accumulation of the cave sediments and the fossils; faunal analyses are provided of the large-mammal assemblages contained in the upper 1.5 m of the deposit; the palaeoecological relationships of the fauna are briefly outlined. Excavation is continuing and further results will be reported elsewhere.

METHODS

The fossil chamber, discovered in 1969 by G. Gartrell and R. Wells (Wells 1975) was found at the end of a narrow rock filled passage (30cm high and 10m long) indicated in Fig. 1. Exposed limb bones, skulls and vertebrae were seen protruding from the sediments throughout the cave. A single path was carefully edged along the southeastern wall of the chamber. On subsequent trips the cave was mapped and the fossil chamber pegged on a 3m (10ft) grid (Fig. 2); each grid square was photographed. A 14m access shaft was sunk from the ground surface to penetrate the southeastern corner of the chamber (Fig. 2). A permanent bench mark was established at the north-western end of the chamber (Fig. 2). As the project continues all sediment and bone is excavated in horizontal quadrats in 15cm depth intervals surveyed from the bench mark. Large bone is relieved in situ, drawn and photographed prior to removal. All sediment surrounding the larger bones is retained, winched to the surface, dried and screened.

Analysis of the small mammal, bird, reptile and amphibian fauna is being undertaken by a number of workers (Tyler 1977; van Tets and Smith 1974; Smith 1971, 1972, 1976), while others are describing the larger elements in the fauna (Wells and Nichol 1977, Wells and Murray 1979, Wells *et al.* 1981).



Fig. 1. Victoria Cave, Naracoorte, South Australia. Access tunnel from the smaller tourist cave on the left is indicated.

VERTEBRATES OF VICTORIA FOSSIL CAVE

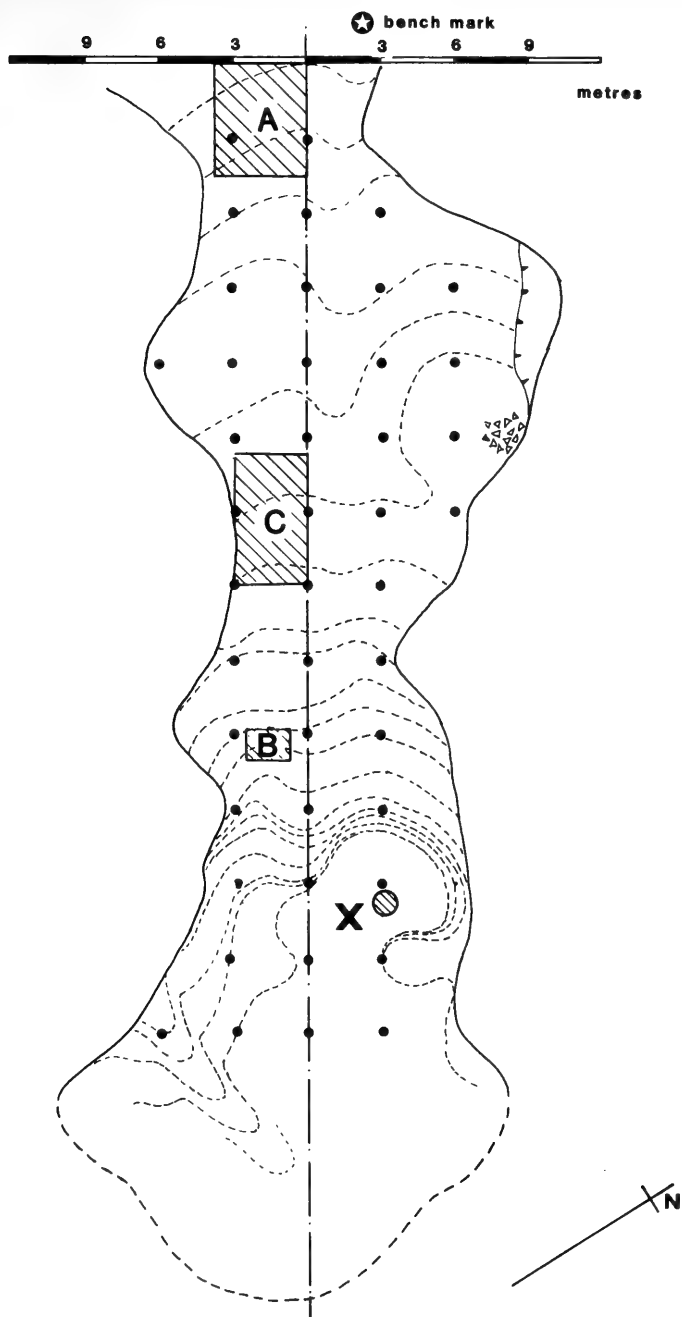


Fig. 2. Floor plan of the fossil chamber. X marks the position of the access shaft. • peg positions for 3 m grid. A, marks position of initial excavation; B, position of stratigraphic pit; C, the third excavation.

The initial site of excavation (A in Fig. 2) was chosen for the presence of partially articulated specimens but it soon became apparent that stratigraphic interpretation would be difficult in this area. Accordingly, following analysis of cores and auger samples from each major grid point a subsurface stratigraphy was constructed and a new site chosen for excavation of a stratigraphic pit (B in Fig. 2). This 1m x 2m shaft was sunk to a depth of 2.7m before progress was halted by a large limestone boulder. Probes inserted along the edge of the boulder penetrated another metre of sediment. The excavation provided important information on sediments and stratigraphy, high yields of small bone but statistically inadequate samples of the larger faunal elements. A third excavation measuring 5m x 3m has now been sunk in 15cm intervals to a depth of 1.5m (C in Fig. 2). The following faunal analysis is confined to the larger specimens from this excavation.

All diagnostic specimens are assigned South Australian Museum (SAM) registration numbers bearing the prefix P. All specimens are allotted grid reference numbers indicating their position in the sediment. A grid reference is in the following form, y-y' Rx-x' D/Dz-z' where R refers to a position right of the y axis when facing the cone of sediment and D/D refers to the depth below the bench mark.

Samples for dating consisted of charcoal and bone. Charcoal was collected with a clean spatula, placed in aluminium foil, and sealed in a plastic container bearing the relevant grid reference. Bone was collected and pretreated for C¹⁴ dating as follows: approximately 1kg of bone from a well defined sedimentary horizon was cleaned in distilled water using nylon brushes and dried at 80°C for 24 hours. Individual bones weighing 20gms or more were selected for amino acid and uranium series dating. The remainder was crushed and ground in a mill. A litre of 50% acetic acid was added to 800gms of crushed bone in an oxygen filled flask. The CO₂ released was bubbled through 50% ammonium hydroxide and collected as ammonium carbonate, this in turn was treated with strontium chloride to form strontium carbonate. The residual bone was then treated with 800mls of 5N HCl and the released CO₂ collected as strontium carbonate. These carbonate samples are referred to as calcite carbonate and apatite carbonate respectively. The insoluble residues were washed and dried and are referred to as Berger collagen (Berger *et al.* 1964). C¹⁴ counting was carried out by H. Polach, A.N.U. Radiocarbon Laboratory.

GEOLOGICAL HISTORY

Victoria Fossil Cave is one of many caves formed in tertiary limestones of South Australia, a low-lying region where topographic relief is provided by a series of old stranded coastal dunes. These dunes consist of sub-parallel ridges of consolidated beach sediments, oriented northwest-southeast and lying parallel to the present coast; they range inland as far as Hynam. They are the result of Pleistocene sea-level changes combined with gentle upwarping of the land surface (Sprigg 1952).

The oldest and most north-easterly of these dunes is the Naracoorte East Dune. It is unusual in having a core of limestone which forms a prominent south-west facing scarp, probably reflecting a fault in the basement rocks (the Kana-winka Fault; Wopfner and Douglas 1971). The Naracoorte East Dune contains a number of relatively deep caves, including Victoria Fossil Cave, formed in the Naracoorte Member of the Gambier Limestone. This is a transgressive shallow-marine unit, deposited during the Oligo-Miocene and consisting of coarse shelly material alternating with finer bryozoal limestone (Ludbrook 1961). Bedding is

subhorizontal, and jointing is well developed in two dominant directions — the major one is parallel to the ridge direction (north northwest) and the other is at right angles (east northeast). Much of the history of cave development can be reconstructed from the caves themselves, and from rock sections exposed in quarries near Naracoorte.

Horizontal cave development has been controlled by the joint pattern (Fig. 1) while roof collapse has generally been along bedding planes, giving rise to flat ceilings in larger caverns. Most of the larger caverns have formed along the major north northwest joint direction, and are connected at floor level by networks of tunnels. This implies that most cave development took place by dissolution of fallen roof blocks at the phreatic zone of an ancient water table, now stranded some six metres above the present valley floors.

The main period of cave formation is believed to have occurred in the Late Miocene/Early Pliocene, following the marine regression of the Mid-Miocene (Sprigg 1952). The Gambier Limestone was subjected to a period of sub-aerial



Fig. 3. Section through the Naracoorte Ridge at Town Quarry. (a) Pleistocene sands of stranded coastal dune with calcrete soil profile; (b) Pleistocene coarse sands and shelly beach deposits, Pliocene Parilla sands; (c) in-filling old karstic surface; (d) Miocene Naracoorte Member of the Gambier Limestone.

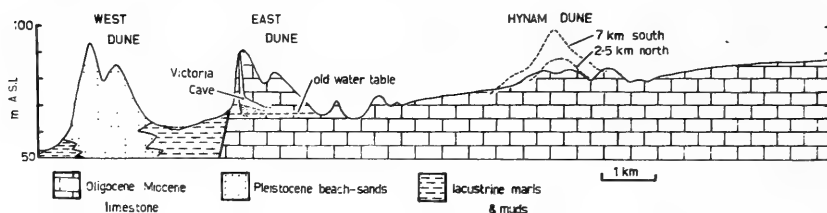


Fig. 4. Transverse section through the Naracoorte dunes: See Fig. 5 for location.

weathering, producing a karst landscape. Solution tubes at the weathering surface (Fig. 3) are filled with Tertiary sediments which are barren of fossils, consistent with their highly leached appearance. Cave development corresponds to a period of high water tables. A large quantity of fine clay with no admixed sand was deposited at the level of the water table, filling the lower tunnels. This was probably the result of local stream incision, and passage of clay-bearing streams through the cave systems.

A transgression in the Pliocene, followed by intermittent regression throughout the Pleistocene deposited a series of beach ridges across the southeast of South Australia (Sprigg 1952).

The transgression eroded the Kanawinka Fault escarpment back to its present location in front of the Naracoorte East Dune creating a sharp drop in the slope of the land (Hossfeld 1950). Given a steady rate of uplift (Sprigg 1952) this would lead to an effective still-stand of the sea at the escarpment and the development of a shoreline facies on the Naracoorte East ridge. The intermittent formation of shoreline ridges shown in the Keith embayment apparently led to the formation of a single dune on the escarpment face consisting of a complex of shoreline facies (Fig. 4).

When the sea finally retreated from the Naracoorte area about 720,000 years B.P. (Cook *et al.* 1977, Idnurm and Cook 1980) the shoreline dunes system began to erode. The limestone between the dunes was lowered but the limestone core within the dunes on the upthrown side of the fault was protected by the overlying sands. The resulting pattern is a series of limestone ridges east of Naracoorte some with vestiges of the younger dune sands trending parallel to the old shorelines (Fig. 5). Much of the capping of the Naracoorte East Dune remains except where proximity to Creeks has caused faster erosion, e.g. at Caves Reserve, Mosquito Creek (Fig. 6).

Erosion of sands from the Naracoorte East Dune allowed sediment and bones to accumulate in the exposed entrances and dolines of the old Tertiary caverns. Preliminary dating suggests that this occurred in the late Pleistocene probably less than 150,000 years B.P.

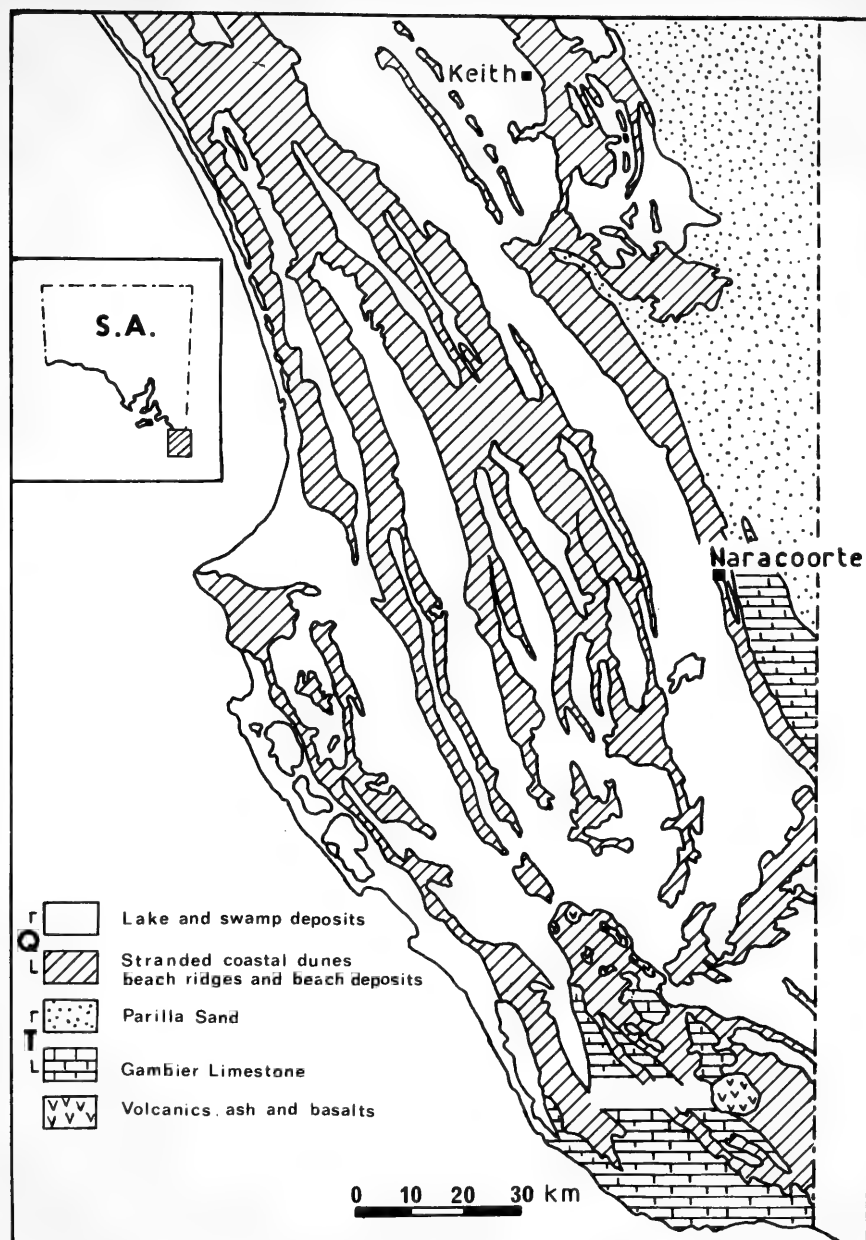


Fig. 5. The southeastern portion of South Australia showing the position of Naracoorte. The caves are formed in the NW/SE trending ridge of Gambier Limestone here covered by stranded coastal dunes.

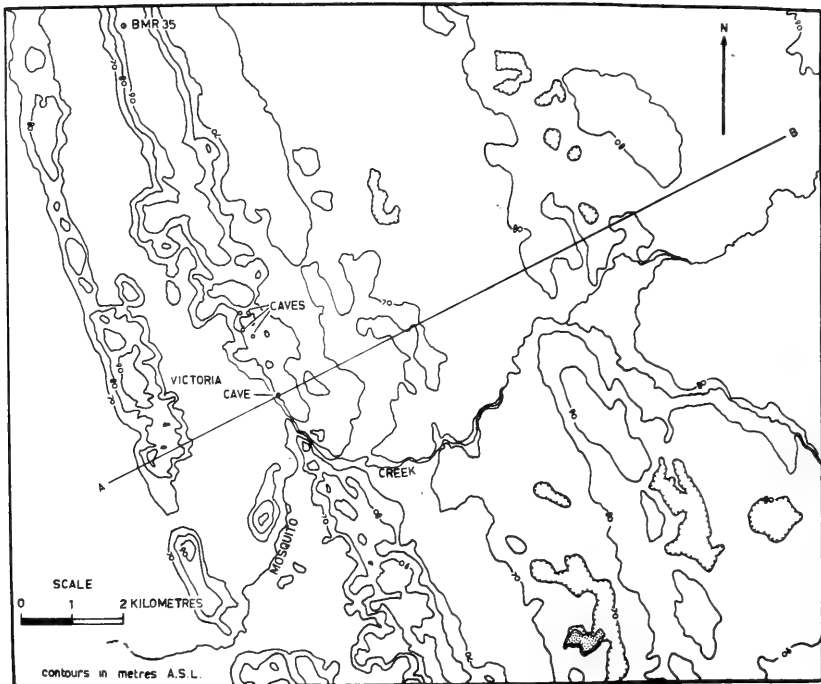


Fig. 6. Topographic map showing relationship of Mosquito Creek to the caves.

The form of the entrance through which the fossils and sediment accumulated in the fossil chamber of Victoria Fossil Cave was determined by pneumatic and hand augering. It was a 50 m long section of the chamber exposed by roof collapse, and was at the base of a doline some 159 m wide possibly caused by erosion of the limestone by water flowing towards the entrance (Fig. 7). Laterally the entrance was steep to vertical with an average width of 10 m.

Both the entrance and the doline are at present filled with sands only slightly affected by a superficial soil development.

CAVE SEDIMENTS

The fossil-bearing sediments have been studied in order to determine their mode of accumulation and the palaeoenvironments that they represent.

In the general case sediment will enter the cave as a result of transport by wind or water, the rate at which it accumulates reflecting surface conditions, such as vegetation and soil cover, water flow rates, etc. Dependent on the amount and rate of water entering the cave, sediments will accumulate either as a cone at the bottom of the entrance shaft or be carried down the developing cone

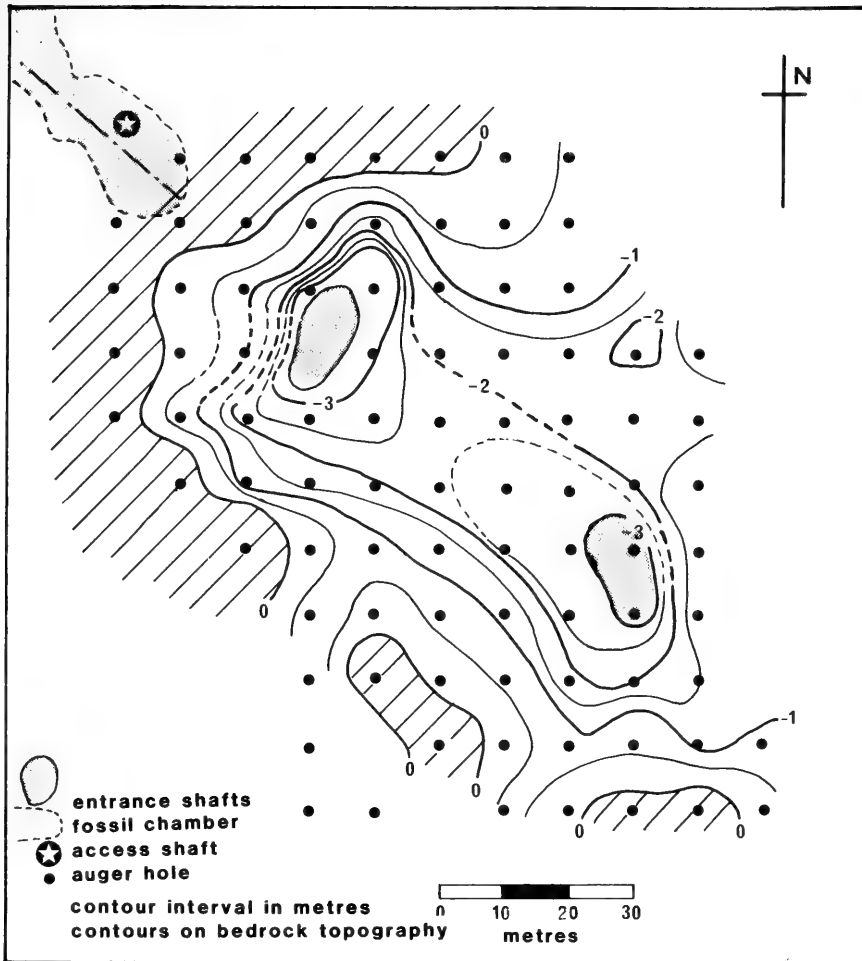


Fig. 7. The buried entrance to the fossil chamber contours determined by hand augering.

slope to be deposited as an alluvial fan (a in Fig. 8). At high flow rates, erosion will take place on the cone slope and even the upper reaches of the fan with subsequent deposition at the further reaches of the fan (b and c in Fig. 8). Mass movements of sediment are most likely to occur following sealing of the entrance shaft by the sediment cone and ponding in the doline. Slumping will occur in a transition zone "T" the width of which will depend on the nature of the sediment and its degree of saturation and the hydraulic head (d in Fig. 8).

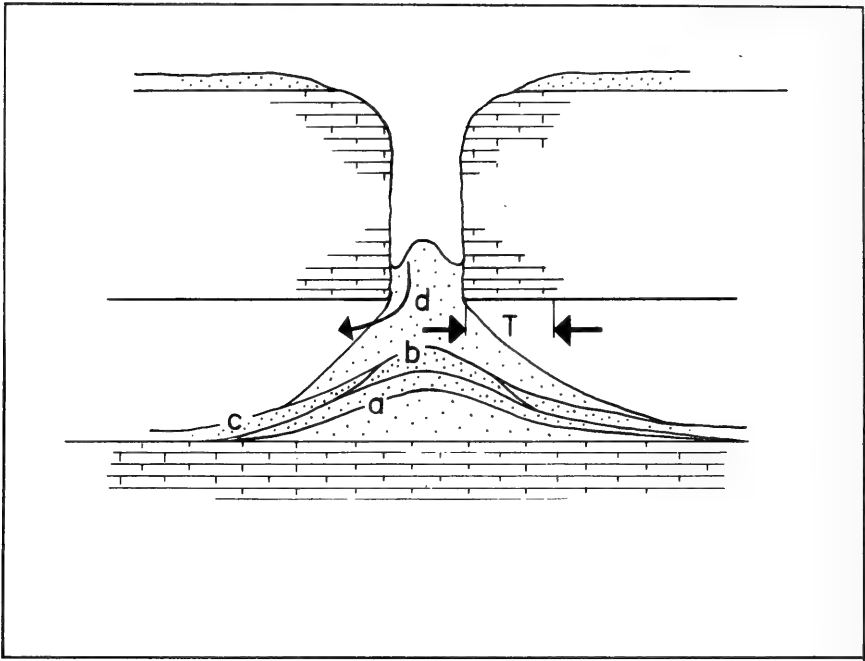


Fig. 8. Model depicting accumulation of cave fill. See text for detail.

Turning to Victoria Fossil Cave the accessible portion of the deposit consists of 28 metres of gently sloping fan and 24 metres of the base of the cone. The angle of slope on the cone is 8° while that on the fan is 3° . Both slopes vary locally due to presence of large limestone blocks which have fallen from the roof.

The sediment in the present surface layer of the cone is buff siliceous clayey sand with numerous limestone fragments, bone and charcoal. Stratigraphic sections show this surface layer lenses out down slope (Fig. 9). Sediments in the surface layers of the fan consist of clean, channel bedded yellow sands grading down slope into tabular layers interspersed with red sand or clay.

THE CONE

Water flow over the surface of the cone is indicated by a channel 1 m wide and 30 cm deep scoured into the surface of the lower part of the cone. Its effect on the floor cannot be seen, as it disappears under the side wall of the chamber. Extensive water flow over the surface of the cone is indicated by areas of several metres of lag deposits of rock and bone lying on the sediment (Fig. 10).

That this lag is not recent rockfall is shown by the staining and slight rounding of the rocks indicating burial for an extensive period. The size of the

VERTEBRATES OF VICTORIA FOSSIL CAVE

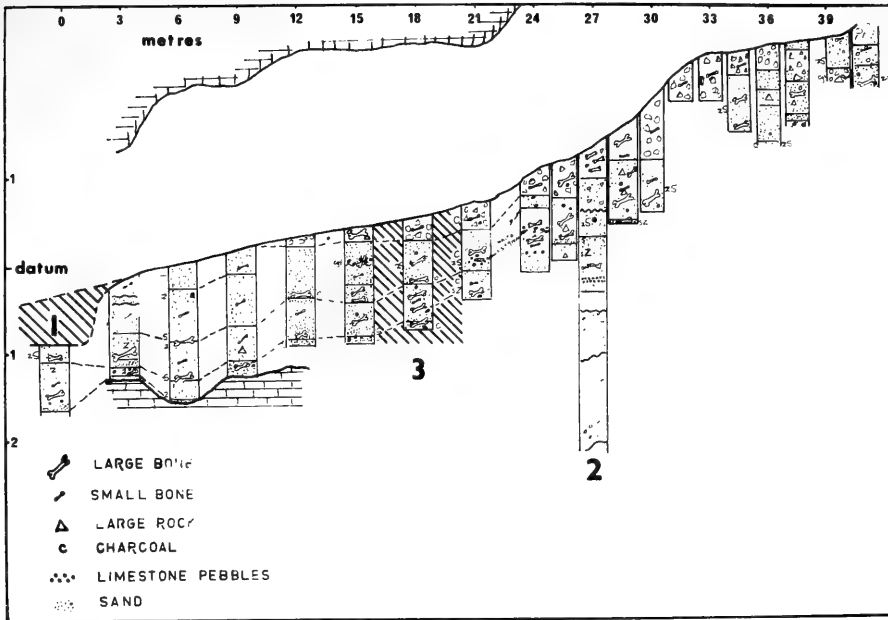


Fig. 9. Longitudinal section through sediments of the fossil chamber. 1, 2 and 3 indicate positions of the initial excavation, the stratigraphic pit and the third excavation respectively.

rocks (up to 15 cm diameter) precludes their downslope transport by the probably maximum water flow rates expected in the cave, although initial emplacement could have been by sediment slump downslope.

The cross-sectional shape of the channel varies and appears to be affected by amount of rock in the sediment — i.e. wide and shallow where rock is abundant, narrow and deep where rock is absent.

Thus depth of erosion on the cone is possibly controlled by the formation of a lag floor, such that continued flows over the cone would leave a lag of bone and rock fragments inhibiting further erosion. Extensive roof collapse has curtailed this process and prevents exploration of the upper part of the cone.

THE FAN

Water flow over the gently sloping fan has cut small channels in the existing sediments close to the base of the cone and the bottom of these channels are filled with a deposit of coarse quartz sand and small bone. Channels in the base of the cone are missing due to erosion by later events, but further downslope the channels grade into tabular layers of clean washed sand interspersed with red sand or clay. This suggests a winnowing process whereby sediments on the cone

and upper part of the fan were sorted into coarse and fine fractions and deposited on the distal part of the fan.

In the upper regions of the fan, interlayered with these channel sands are layers of buff or brown clayey sand containing rock fragments and bone.

If the channel sands are true lag deposits the clay and sand in the distal part of the chamber would be the winnowed fines deposited in the low velocity or temporarily ponded stages of the flow.



Fig. 10. View of the surface of the fossil chamber showing the distribution of rock and bone lag.

INTERPRETATION

It is first necessary to explain the mode of emplacement of the source material, the unsorted sediments covering the cone and upper reaches of the fan. These sediments are buff clayey silty sands with rock fragments and large bones.

A single mass movement of sediment, bone and rock is ruled out by presence of small channels preserved completely within these sediments on the upper reaches of the fan. The grain sizes and lack of sorting suggests low energy deposition but cannot account for the transport of rock fragments and large bone.

The best explanation appears to be a *series* of saturated mud flows only a few centimetres thick occurring down the cone and over the upper reaches of the fan with very little water flow between the events. Sediment which slumps down an accreting cone would continue out over the upper parts of the fan until momentum was lost. The extent of flow over the fan would be determined by the size of the slump and could continue to distal parts of the fan given suitable fluidity and momentum.

Similarly free water movement could cause deposition of winnowed sediments at any point on the fan. Both situations could be localised and contemporaneous on different areas of the fan. The sediments would then be facies equivalents.

The second requirement is to determine the source of the clean yellow sands. Are there yellow sands in the cone or are they derived from a sediment which originally had a high clay content? The apparent absence of lag deposits in these sediments suggests little erosion of the underlying beds and implies a predominantly depositional or accretionary regime.

Sediments exposed in the lower part of the stratigraphic pit (Fig. 9) consist of well-sorted quartz sands with a low clay content, their colour varies from grey brown to yellow. Similar quartz sands occur at the ground surface filling the entrance shaft and doline. Thus a source for the clean yellow sands of the fan does exist. The absence of winnowed clay in the channel sand of the fan along with the absence of a bone or limestone lag suggests a different source to that of the buff clayey sands. Furthermore it points to different environmental conditions governing the formation of the two types of sediments and implies a significant separation in time.

If the rock fragments in the sediments have originated mainly from spalling of the ceiling of the cave then high densities of rock in the buff sediments may indicate a prolonged exposure at the surface. In other words, the buff coloured clayey sands containing these fragments may be associated with a prolonged period of accumulation.

In the course of the work it was noticed that the continued fretting of the ceiling of the cave produced a fine limestone dust which settled on the exposed

sediments. An analysis of the soluble carbonate content of the sediments may then give some estimate of the relative time of exposure of any given horizon. Sediments were sieved through 1 mm mesh in 5 gm samples selected by cone and quartering. Samples were dried at 75°C 3 hours, digested in dilute HCl, filtered and redried and the % acid soluble content determined. Peaks in the acid soluble content occur at the surface and at levels 6, 11, 17. Troughs occur at levels 9, 12, 13 (Fig. 11).

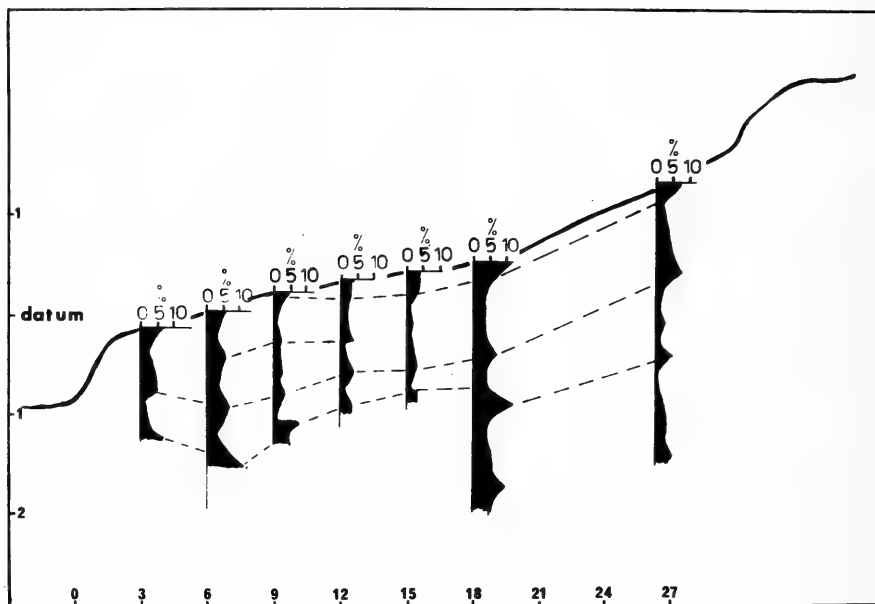


Fig. 11. Longitudinal section of the Victoria Cave fossil chamber showing the % acid soluble content of sediments from cores.

A comparison between the acid soluble content of the sediments, the stratigraphy and bone density is illustrated by Figs. 9 and 11. Peaks in acid solubles correspond with poorly sorted buff sediments containing limestone clasts and bone, while troughs in acid solubles correspond to relatively clean mottled orange yellow sand layers with sparse bone and limestone clasts.

The high clay content of the buff poorly sorted sediments suggests the source was a soil, which implies a lengthy period of stability in the doline above. Such stability would not be compatible with the existence of the fast water flow evident in the channeled yellow sands so a separate period of formation for the two types of layers is supported. Soil development is very limited in the doline at the present time, and if the cave were to open now, yellow and orange quartz sands would be washed into the cave in large quantities. Also, significant move-

ment of sand into the doline would probably indicate unstable, arid surface conditions. The lack of clayey soil development at the present time might be taken to indicate that the climate which led to the formation of these clay soils was much more humid than conditions now prevailing.

The conclusion from the data is that the fossil bearing beds originated in a series of depositional stages comprising two events:

- (1) clay soil formation with bone and rock accumulation with the soil products on the cone and periodic slumps onto the fan;
- (2) sandy soil formation with fast sedimentation on the cone and periodic water flows onto the fan.

The lower part of the sequence has been exposed in the three metre deep stratigraphic pit and consists of a sequence of poorly-sorted to partly-sorted quartz sands containing variable quantities of clay, bone, charcoal and organic remains. The top of most beds is erosional and clay clasts are common in the upper units. Cross and slumped bedding is visible in the lower units. The thickness varies greatly over the metre wide section, and some units are in part completely eroded. The depositional dip is much steeper than that of the overlying beds, and this may be caused by the presence of a large block of limestone buried a few metres upslope, but alternatively may indicate that the source was a solution tube in the ceiling now filled with clay and rock, a few metres upslope. The lower units may have originated as a cone formation from the solution tube, but the dip and thickness of the upper units indicates a more distant source, probably the entrance shaft. The sediments of this lower part of the sequence appear to be sandy soil material which has undergone little reworking or sorting in the transport process, and some appear to be similar to the present day soils. The bone is bleached and mineralised and appears to have been exposed sub-aerially for some time in a dry environment. This would accord with the lack of clay and soil development. Analysis of the fauna from this part of the sequence must await further excavation.

THE BONES

An understanding of the process by which the sediment and bones accumulated is critical to placing the fauna in a time stratigraphic context. Evidence of reworking and sorting of some layers indicates the flowing water was important in the deposit, while poorly sorted sediment in other layers implies mass movement of sediment and bone.

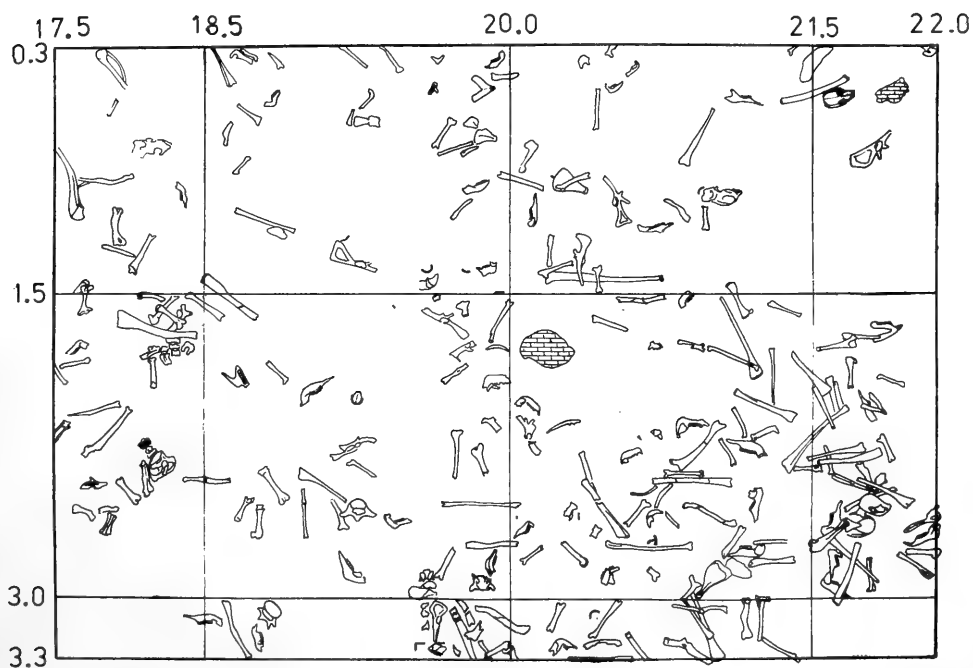
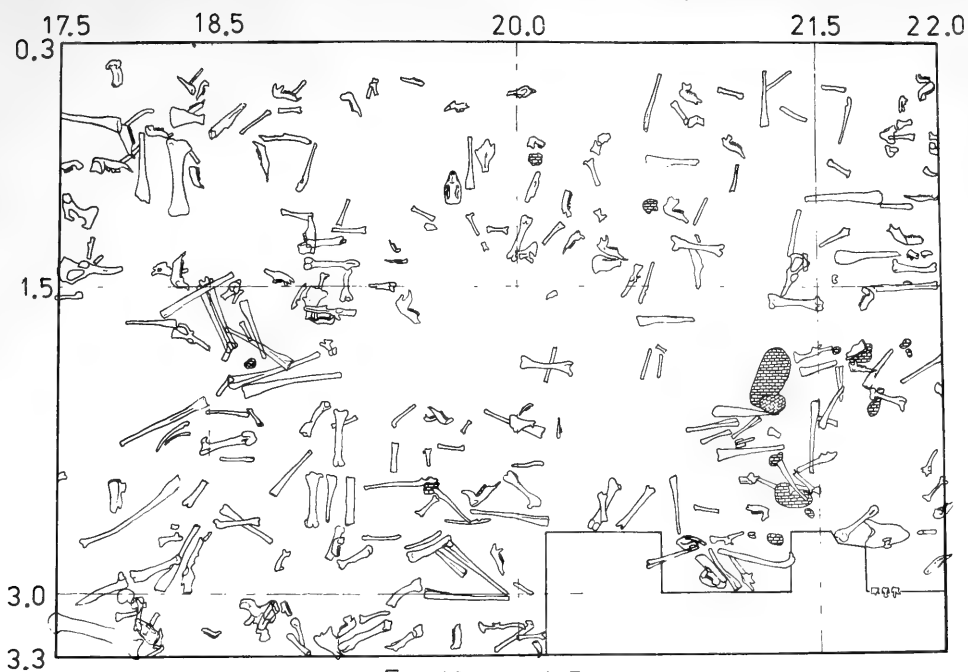
Experiments to simulate filling of the cave were carried out by pouring cave sediment and small mammal bones through an orifice and into a tray conforming approx. to the outline of the fossil chamber. Using dry sand produced a cone of sediment upon which bones tended to slide down slope, large end leading, their long axes aligned with the direction of sediment flow. A few of the more symmetrical bones sometimes rolled part of the way, long axes transverse to the

direction of sediment flow. Pouring water gently through the simulated cave entrance led to the development of channels with small levees down the surface of the cone terminating in a number of coalescing fans. If the flow was very gentle bone tended to be left as a lag on the surface of the cone. As the flow increased bone was moved onto the fans maintaining the same orientation as on the cone. With successive washings a bone lag developed at the base of the cone and the upper reaches of the fan. The expected winnowing and sorting of sediment and bone occurred down the fan. High water flows resulted in the rapid development of scours at the base of the cone. These scours migrated back against the current and led to the collapse of portions of the cone. Bone in these channels was moved quite rapidly, often tumbling rather than rafting, to collect in a jumbled mass at the base of the cone or be swept out across the fan.

Examining the situation within the cave: almost without exception the large elongate bones such as tibiae and femora lie with long axes parallel to the bedding plane, large end down slope (Fig. 12). Rose diagrams (Fig. 13) indicate the frequency of particular orientations. The predominant alignment is with the long axis of the cave with a secondary alignment at right angles to the first. These observations are all indicative of low energy transport as under a higher energy regime one might expect bones to be less well preserved and for a significant portion to lie in unstable positions, i.e. dipping at high angles to the bedding plane. Skulls, when complete are also aligned with the long axis and are often so well preserved as to retain the paper-thin turbinial bones. Damage to such skulls is usually restricted to the overhanging tips of the nasals. Juvenile skulls tend to collapse along the suture lines. Scapulae with their large surface area are particularly susceptible to post mortem damage, yet even these are well preserved, their laminae lying parallel to the bedding planes. Notwithstanding the excellent state of preservation of the bone most of the specimens are disarticulated, indeed most partially articulated material has been found either at the distal end of the fan or against the wall of the cave.

When analysing the large bone from any one stratum of pit C there are consistent differences in the ratios of the major elements. For example, there are on average twice as many tibiae as femora while scapulae, humeri and pelves are approximately equally represented although the total number is, on the average, about half that the femora. If it were not for the excellent state of preservation of the bone and the absence of all but a few rodent gnawings one could be tempted to attribute these disparities to the action of predators. We consider it far more likely that these differences are a reflection of the ease of transport of different bone morphologies. Further evidence of this hypothesis comes from an analysis of the skulls and jaws from this excavation. If the two components are reduced to the minimum number of individuals then jaws exceed skulls in the ratio 2.2:1. In the absence of a predator that selectively destroyed skulls the disparity between skulls and jaws must be due to differences in hydraulic per-

VERTEBRATES OF VICTORIA FOSSIL CAVE



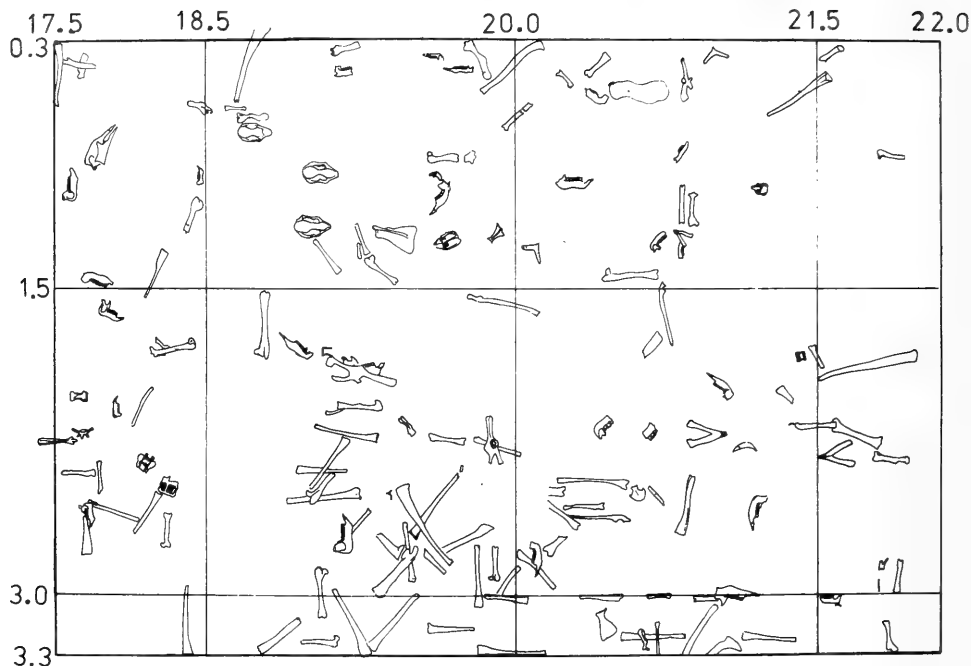


Fig 12.level 7

Fig. 12. The distribution of larger bones from three adjacent levels (5, 6 and 7) in excavation C.

formance. We would then propose that for the large animals the cave acted as a pitfall trap.

The pitfall hypothesis may be tested by an examination of the age classes of the fauna. Van Valen (1963, 1964) and Voorhies (1969) have used age frequency distributions to distinguish catastrophic from attritional mortality. Using the method of Kirkpatrick (1965) we determined the age/frequency distribution for *Macropus rufogriseus* specimens, a common element in the fauna. The curve (Fig. 14) is indicative of a catastrophic accumulation and is consistent with the hypothesis of a pitfall, trapping animals at random. Similar distributions based on tooth eruption only are shown for other common extant and extinct species in the fauna in Fig. 15.

Our conclusions are that (1) the large animals fell into the cave via a pitfall, (2) the skeletons of those that perished on the cone were buried by incoming sediment, redistributed and disarticulated either by mass movement or gentle rafting when water washed down the cone or a combination of both, (3) skeletons of animals that perished on the distal parts of the fan were subject to even less water movement and hence partial articulation was maintained, and (4) that in

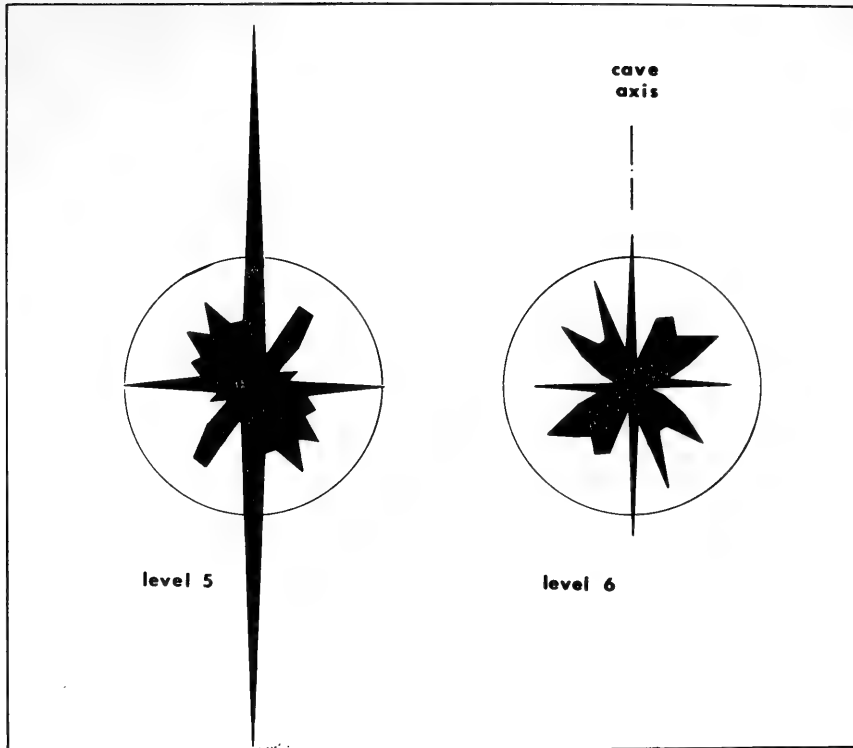


Fig. 13. Rose diagrams depicting the frequency of alignment of bones from two levels chosen at random.

the absence of other evidence the proportion of particular skeletal elements within a local area of any sedimentary horizon is correlated with the ease of transport of those elements.

Accepting these conclusions a number of problems arise. Clearly if the hydraulic performance of various skeletal elements affects their distribution within a given stratum, then an adequate reconstruction of the faunal assemblage will require samples from each facies of that sediment. Furthermore, continual low energy water flows over the cone and fan could result in the development of a lag of bone spanning a considerable period. A subsequent high energy flow could redistribute this lag, simultaneously burying it in younger sediment. This problem is considered further when we come to a discussion of dating.

Thus far we have confined our analysis to the larger elements of the fauna. Undoubtedly the same hydraulic processes have led to redistribution of the bones of the smaller vertebrates although there is evidence to suggest that initially many may have been brought in by predators using the cave as a den or roosting

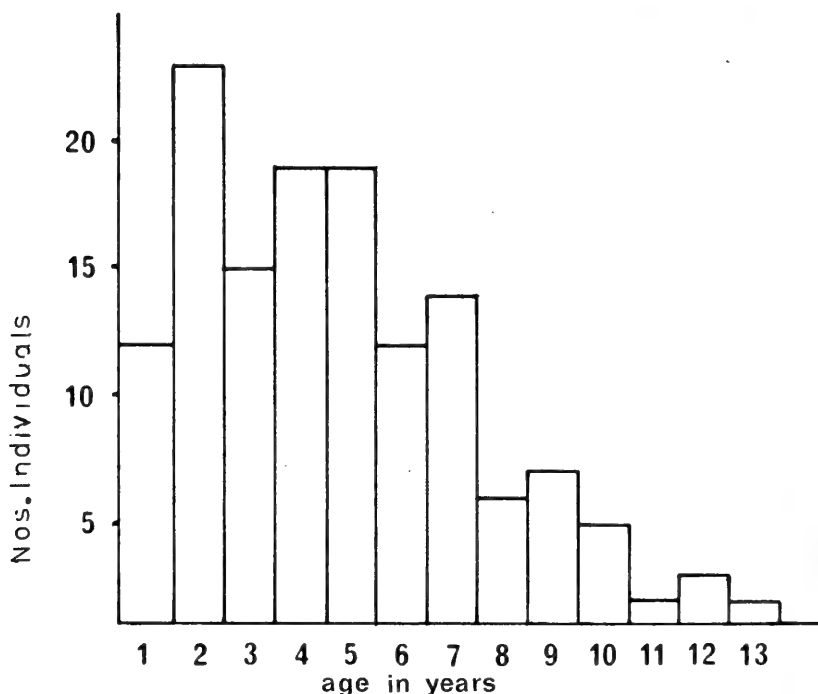


Fig. 14. The frequency of yearly age classes of *Macropus rufogriseus* skulls from excavation C.

site. Smith (1971, 1972) noted that there was considerable variation in the proportion of adults among the smaller species, e.g. the larger of these, *Bettongia penicillata* and *Potorous apicalis*, were represented almost entirely by juveniles as was the large bandicoot *Perameles gunnii*. Yet in the smaller species, *Isodon obesulus* and *Potorus platyops*, adults and juveniles were found in about equal numbers, while the small dasyurids (*Antechinus* spp., *Sminthopsis* spp.) and the petaurids and burramyids were almost all adults. Smith suggests that this biased age structure is suggestive of a predator accumulation. In her discussion of likely predators she eliminates *Thylacinus cynocephalus* on the grounds that it was likely to take larger prey. We would also eliminate this species on the basis of its poor representation in the fauna. Smith also uses the low incidence of *Dasyurus maculatus* to suggest it was not the predator responsible, while the high incidence of juvenile *Dasyurus viverrinus* as being indicative of a prey rather than predator species. Smith suggests that the small mammal remains probably accumulated from owl pellets.

VERTEBRATES OF VICTORIA FOSSIL CAVE

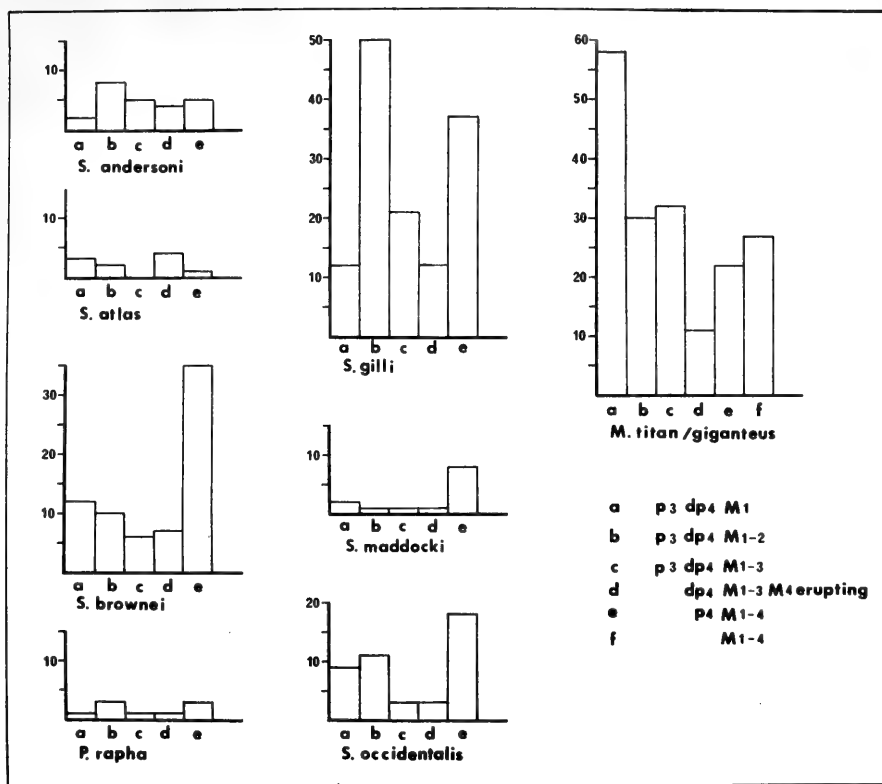


Fig. 15. The frequency/age distribution for other macropodid species from Victoria Cave fossil chamber. Age classes represented by tooth eruption sequence.

THE FAUNA

The 78 species of vertebrates so far identified from the top 1.5 m of sediment are listed in Table 1, 77% are extant while 23% are no longer to be found in South Australia. Mammals in this latter group are to be found in the dense understorey of sclerophyll forests. The exceptions are the Thylacine which has only been recorded from Tasmania in historic time and *Perameles bougainville* from the heaths and coastal dunes of W.A. The absence of the remainder in this area today may be due to climatic shifts but may equally be due to the extensive clearing of the understorey during the early days of settlement. Certainly the latter point is suggested as the reason for the disappearance of *Pesoporus wallicus* in historic time.

TABLE 1.

SPECIES REPRESENTED IN THE TOP 1.5 M OF PIT 3 († EXTINCT, * EXTANT
BUT OUTSIDE HISTORIC RANGE)

MARSUPIALIA

Family — THYLACINIDAE	* <i>Thylacinus cynocephalus</i>
— DASYURIDAE	† <i>Sarcophilus cf. lanianus</i>
	* <i>Dasyurus maculatus</i>
	* <i>D. viverrinus</i>
	<i>Antechinus flavipes</i>
	* <i>A. swainsonii</i>
	* <i>A. stuartii</i>
	<i>Sminthopsis murina</i>
	<i>S. crassicaudata</i>
— PERAMELIDAE	<i>Isodon obesulus</i>
	* <i>Perameles gunnii</i>
	* <i>P. bougainville</i>
— PETAURIDAE	<i>Pseudocheirus peregrinus</i>
	<i>Petaurus breviceps</i>
— BURRAMYIDAE	<i>Cercartetus nanus</i>
— PHASCOLARCTIDAE	<i>Phascolarctos cinereus</i>
— VOMBATIDAE	<i>Vombatus ursinus</i>
— MACROPODIDAE	<i>Macropus giganteus</i>
	† <i>M. titan</i>
	<i>M. rufogriseus</i>
	† <i>M. greyi</i>
	<i>Wallabia bicolor</i>
	* <i>Lagorchestes cf. conspicillatus</i>
	* <i>Bettongia penicillata</i>
	* <i>B. gaimardi</i>
	* <i>Potorous apicalis</i>
	† <i>P. platyops</i>
	† <i>Sthenurus atlas</i>
	† <i>S. andersoni</i>
	† <i>S. gilli</i>
	† <i>S. maddocki</i>
	† <i>S. occidentalis</i>
	† <i>S. brownei</i>
	† <i>Procoptodon rapha</i>
	<i>Protemnodon roechus</i>
— THYLACOLEONIDAE	† <i>Thylacoleo carnifex</i>
— DIPROTODONTIDAE	† <i>Zygomaturus trilobus</i>
	† <i>Palorchestes azael</i>

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RODENTIA

- MURIDAE
 - Pseudomys australis*
 - **P. albocinereus*
 - **P. cf. fumeus*
 - **Mastacomys fuscus*
 - Conilurus cf. albipes*
 - Rattus sp.*

MONOTREMATA

- TACHYGLOSSIDAE †*Zaglossus ramsayi*

AVES

- DROMAIIDAE *Dromaius cf. novaehollandiae*
- MEGAPODIDAE *Progura naracoortensis*
- Leipoa ocellata*
- PHASIANIDAE *Coturnix pectoralis*
- C. australis*
- TURNICIDAE *Turnix sp.*
- T. varia*
- PEDIONOMIDAE *Pedionomus torquatus*
- RALLIDAE *Rallus philippensis*
- CHARADRIIDAE *Peltohyas australis*
- SCLOPACIDAE *Tringa glaveola*
- Gallinago hardwickii*
- Calidris ruficollis*
- PLATYCERCIDAE *Pesoporus wallicus*
- TYTONIDAE *Tyto novaehollandiae*
- GRALLINIDAE *Grallina cyanoleuca*
- CRACTICIDAE *Gymnorhina tibicen*

Van Tets and Smith (1974) also report a sheath bill *Chionis minor* but this identification has been challenged by Olson (1976).

REPTILIA

- BOIDAE †*Wonambi naracoortensis*
- ELAPIDAE *Pseudonaja cf. nuchalis*
- Notechis cf. scutatus*
- Pseudechis cf. porphyriacus*
- VARANIDAE *Varanus varius*
- V. gouldii*
- SCINCIDAE *Trachydosaurus rugosus*
- Tiliqua nigrolutea*
- cf. Sphenomorphus tympanum*
- Egernia cf. whitii*
- AGAMIDAE *Amphibolurus cf. barbatus*
- CHELIDAE *cf. Emydura macquarii*

AMPHIBIA

— HYLIDAE

Litoria ewingii

— LEPTODACTYLIDAE

Limnodynastes cf. dumerili

Ranidella signifera

Geocrinia cf. laevis

MOLLUSCA

Paralaoma sp.

Combining the preferred habitats of all the extant vertebrate species suggests an environment of dry sclerophyll forest, savannah woodland and substantial areas of heath, wet and dry grassland and mudflats. Indeed, an environment typical of the southeast of South Australia at the time of settlement.

Similarly, a reconstruction of the past environment based on the adaptations revealed by the extinct Sthenurine kangaroos and Diprotodontids (Tedford 1966, Wells 1978) suggests the presence of grasslands and shrublands.

AGE OF THE FAUNA

This initial analysis is confined to the top 1.5 m of pit C. Comments relate to the remains of species the size of the red-necked wallaby (*Macropus rufogriseus*), adults 4 kg or larger. Palaeontological excavations are usually undertaken on the initial assumption that one is dealing with an accretionary sequence. Fossils are then assigned to a sedimentary horizon by observing changes in lithology during the process of excavation. The sediments of Victoria Fossil Cave pose a special problem; comprised largely of dune sands with variation in the amount of admixed clay and organic material, differences in lithology are often quite subtle and almost impossible to detect on a small scale under artificial light. Accordingly, sediment and bone was removed in quadrats measuring 60 cm x 30 cm (long axis aligned with that of the chamber), in horizontal intervals of 15 cm. It was only possible to determine the conformable nature of the sediments, their dips and strikes, when large areas of the pit wall were exposed. A computer model was devised to account for the observed changes in dip in both transverse and longitudinal directions with depth. All specimens from each horizontal quadrat were then assigned a stratigraphic depth. Six hundred diagnostic specimens (skulls and jaws) representing a minimum of 232 individuals were used in this analysis. The frequency-distribution by species in each 15 cm level is shown in Fig. 16. For well-represented species it approximates a bell-shaped curve, low numbers in levels 1 and 2 building to a peak at level 6 and diminishing again by levels 9 and 10. A comparison of the species distribution with that for acid solubles indicates an inverse relationship for the top and bottom layers of the pit and a positive correlation for level 6. If the high acid soluble content is indeed a reflection of a hiatus in sedimentation it would suggest that the peak in numbers of individuals in level 6 may represent a bone lag rather than any change in fauna density outside the cave.

VERTEBRATES OF VICTORIA FOSSIL CAVE

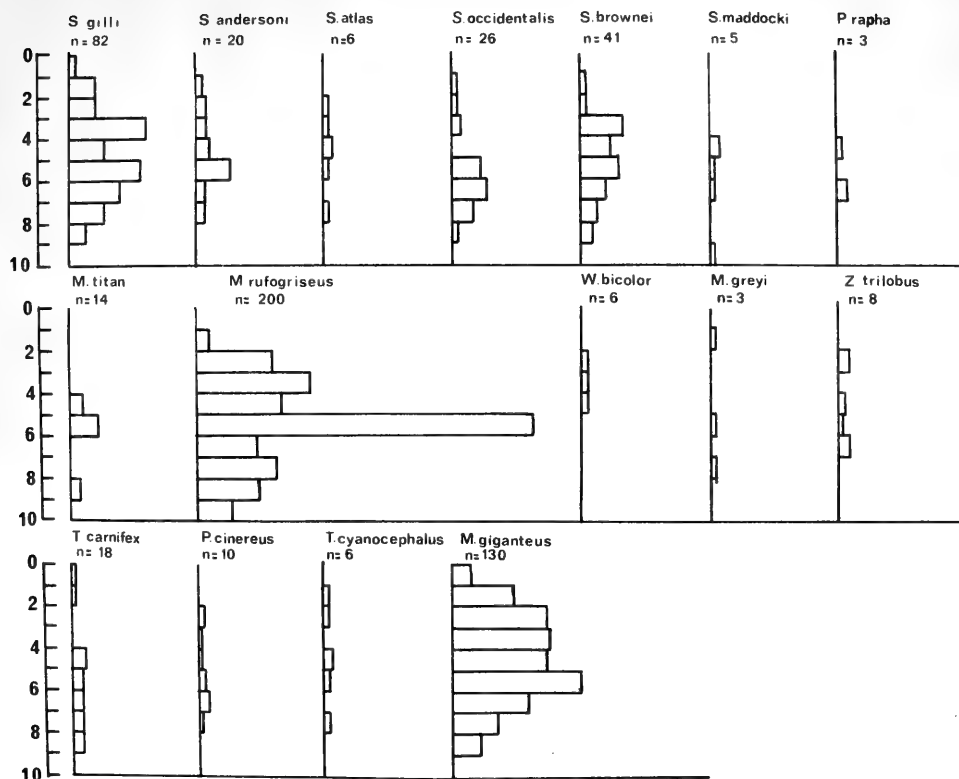


Fig. 16. The frequency distribution of large species in each 15cm level of excavation C.

Alternatively the peak in diagnostic elements at level 6 may be a reflection of the hydraulic regime, different species being represented in levels 1 and 2, 9 and 10. Some evidence in support of the lag hypothesis may be gained from an examination of the various dates obtained for bone and charcoal from these levels, Table 2.

There is a gradation of ages in the charcoal profile, however, the small sample size has led to a large error or minimum ages only have been obtained. Nonetheless, the evidence supports the assumption of an accretionary sequence. Little can be deduced from the collagen dates due to their enormous error factor, a situation which may be resolved by processing larger samples. Nonetheless, it would appear that bone from all levels is considerably older than the associated charcoal suggesting a lag accumulation. The bone carbonate and apatite dates indicate a gradation in soil carbonate ages down the profile which could result from a dynamic equilibrium between the soil carbonate and bone apatite

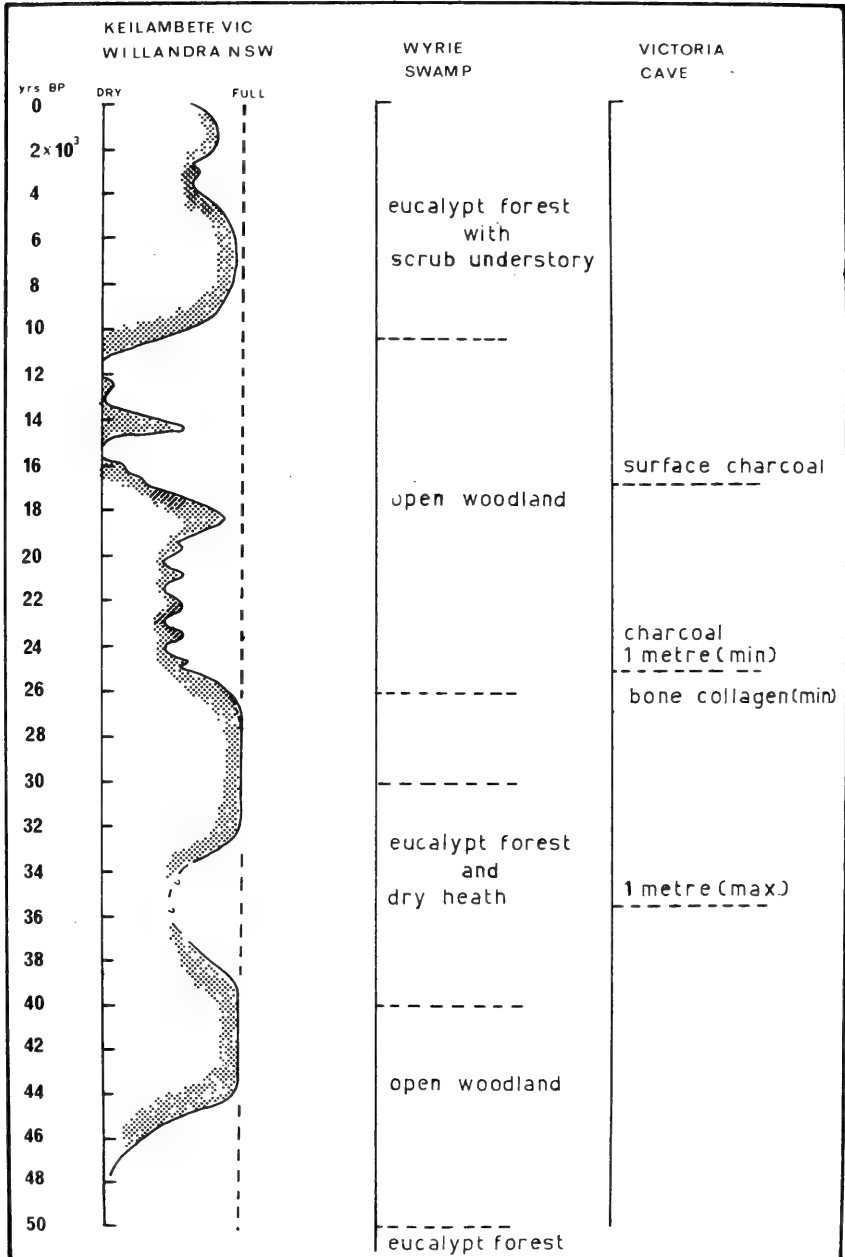


Fig. 17. The relationship between events represented in the top metre of sediment from Victoria Fossil Cave fossil chamber to hydrological and palynological changes in the late Pleistocene of Southern Australia.

VERTEBRATES OF VICTORIA FOSSIL CAVE

TABLE 2. C^{14} ages of charcoal and bone fractions from levels 1 and 2 and 6 and 7 from pit 3, Victoria Fossil Cave, Naracoorte.

Level	Sample No.	Fraction	Age Yrs B.P.
1 and 2	ANU 1858	Charcoal	16,700 { +3,000 -2,180
	ANU 1855	Calcite CO_3	
	ANU 1856	Apatite CO_3	23,000 ± 600
	ANU 1857	Berger "Collagen" (acid insol.)	>23,900 (~38,400)
<hr style="border-top: 1px dashed black;"/>			
6 and 7	ANU 1852	Charcoal	>25,100 (~35,500)
	ANU 1859	Calcite CO_3	6,650 ± 100
	ANU 1860	Apatite CO_3	19,300 { +1,690 -1,390
	ANU 1861	Berger "Collagen"	>25,100 (~35,500)

in an open system, or be due to incomplete removal of contaminatory secondary carbonate in the pretreatment stage (H. Polach, pers. comm.).

Although improvement in sampling may reduce the dating error, this will not help to resolve the faunal succession short of dating sites of individual specimens from each layer. Both racemisation and uranium series dating require samples of 12 gms or less, making it possible to date individual specimens. Preliminary dates on bone from levels 1 and 2 are for uranium series 125,000 BP U/Th and 150,000 U/Pa (H. Veeh, pers. comm.), while preliminary racemisation dates for bone from the same levels are 50,000 and 70,000 BP ± 20% (J. Bada, pers. comm.). We are thus forced to treat levels 1 to 10 as a single biostratigraphic unit while paradoxically we can resolve the sediments into smaller units suggestive of changes in rainfall/evaporation operating outside the cave.

Although all dates fit well within the time range allowed by the geological model for accumulation of the fauna, the disparate values obtained point to the need for great caution in interpreting faunal succession. Fig. 17 relates the time span of events represented by the top metre of sediment to the sequence of hydrological and palynological (Bowler et al. 1976, Dodson 1977) changes in the late Pleistocene of Southern Australia. The pollen data is from Wylie Swamp 80 km south of Victoria Fossil Cave. These data indicate that during the period represented by the sediments (charcoal dates), the inland lakes have passed from a period of high water level to an ephemeral condition and finally dried up, while the vegetation of the coastal plain has passed from eucalypt forest with a scrub understory to an open woodland. Similar climatic fluctuations are reflected in the Victoria Cave sediments, while the large fossil fauna is dominated by browsing herbivores and, although possibly spanning a greater time, is not inconsistent with the pollen data. The decline of the scrub understory with increasing aridity is more likely to be reflected in an analysis of the small mammal fauna.

ACKNOWLEDGEMENTS

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Fish, Amphibians and Reptiles from the Etadunna Formation, Miocene of South Australia

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ABSTRACT

The Middle Miocene Etadunna Formation near Lake Palankarinna, South Australia, has yielded records of lungfishes (Ceratodontidae, *Neoceratodus* sp.), catfishes (Ariidae), percoids (Percichthyidae), frogs (Hylidae, *Litoria* sp.), turtles (Chelidae, *Emydura* sp.), lizards (Scincidae, *Egernia* sp.; Varanidae, *Varanus* sp.) and crocodilians (unidentified teeth). These form part of the Ngapakaldi local fauna; the records of *Egernia* and *Varanus* are the earliest for these genera in Australia. Among the fossil groups identified, only percichthyid fishes and the lizards *Egernia* and *Varanus* occur in the area today.

The Middle Miocene Wipajiri Formation, which overlies the Etadunna Formation in the Lake Ngapakaldi area, South Australia, has also produced remains of *Egernia*, as well as specimens of the related genus *Tiliqua* and fragmentary material of a presumed agamid lizard; these form part of the Kutjamarpu local fauna, also of Middle Miocene age.

INTRODUCTION

In spite of intensive field work by numerous parties, the lower vertebrate fossil record from Cenozoic Australia remains sparse. In particular, microfossil material of lizards and frogs is of great interest in helping to determine the time of emplacement, past diversity and zoogeographic affinities of these groups in Australia. A number of studies by Australian workers have been published (e.g. Molnar 1982; Tyler 1982a,b); others are in progress and it is hoped that knowledge of Australian paleoherpetology will soon be more extensive (see Rich and Thompson 1982).

So far, one of the richest samples yet obtained is from the type section of the Middle Miocene Etadunna Formation near Lake Palankarinna, South Australia. University of California (Riverside) localities RV-7230 and RV-7247 have produced the material discussed here. Lake Palankarinna is south of Cooper Creek and about 30 km south of Etadunna Station at approximately latitude 28°47'S., longitude 138°25'E. The University of California localities are among those that have produced the Ngapakaldi local fauna (Stirton *et al.* 1961). RV-7230 is equivalent

to Tedford Quarry, officially University of California (Berkeley) locality UCMP V-5375 of Stirton *et al.* (1961) and RV-7247 is about 1.5m stratigraphically below RV-7230 at the same locality. The localities are in green argillaceous sandstone in the upper half of the Etadunna Formation. The fossils were recovered by washing and screening techniques used by Michael Woodburne and party; the repository of specimens is in the Museum of Paleontology, University of California (Riverside).

DESCRIPTIONS OF FOSSILS

The lower vertebrate remains include lungfish teeth, abundant disarticulated teleost bones, and relatively rare lizard and frog bones, as well as a few teeth of small crocodilians.

ORDER DIPNOI

Family Ceratodontidae

Neoceratodus sp.

Material: UCR 20810, tooth; other unnumbered specimens.

Comments: The presence of this lungfish in the Ngapakaldi fauna is shown by the occurrence of a number of characteristic teeth referable to the living genus, which has a record extending back to the Early Cretaceous in Australia. *Neoceratodus* was widely distributed in eastern Australia during the Cenozoic although it is restricted today to southeastern Queensland (for a summary of its past distribution see Williams 1980; Long 1982; Long *et al.* 1982). Long *et al.* (1982) cited the presence of *N. eyrensis* and *N. gregoryi* in about equal proportions in the Etadunna Formation but the present specimens have not yet been identified to species. The latter authors also identified rare *Ceratodus wollastoni* in the Etadunna Formation; no examples of this species occur in the UCR collection.

ORDER SILURIFORMES

Family Ariidae

unidentified genus and species

Material: UCR skull, fin and vertebral elements.

Comments: Abundant remains of this family of catfishes occur in the localities bearing the Ngapakaldi fauna, and have been identified by Camm Swift (Los Angeles County Museum of Natural History). The family is not represented in the Lake Palankarinna area today; they are found in the northern river systems but do not at present occur in the Lake Eyre drainage (P. Kailola, pers. comm. 1983). The Ariidae is a marine group that frequently enters fresh waters in tropical regions (McDowell 1980). The related family Plotosidae may also be represented, but more detailed study is needed to confirm this (Camm Swift, pers. comm. 1981).

LOWER VERTEBRATES FROM THE ETADUNNA FORMATION

ORDER PERCIFORMES

Family Percichthyidae
unidentified genus and species

Material: UCR skull, vertebral and fin elements.

Comments: The most abundant fish fossils in the Ngapakaldi fauna localities are referable to the family Percichthyidae (temperate basses), and also have been identified by Camm Swift. This family still occurs in the Lake Palankarinna region; it is a marine group that enters brackish and freshwater drainages in temperate and tropical areas. It is possible that some of the material may be referable to the related family Theraponidae (tiger perches), but additional study is necessary to confirm this (Camm Swift, pers. comm. 1981).

ORDER ANURA

Family Hylidae
Litoria sp.

Referred material: UCR 20811, ilium; 20812, humerus; 20813, sacral vertebra; other unnumbered elements including maxillary fragments, a premaxilla, a distal tibia and trunk vertebrae.

Comments: Identification of the frog material is difficult, owing to its fragmentary nature and the similarities between elements of hylids and leptodactylids. Based on humerus, ilium, tibiofibula and sacrum size and morphology, only one group appears to be represented.

The single broken ilium is from a small individual, and resembles that of hylids in having a low, laterally-directed dorsal protuberance and a generally triangular acetabular region, instead of the large, truncated acetabular expansion seen in leptodactylids. Referral to the extinct genus and species *Australobatrachus ilius*, the type specimen of which comes from RV-7230 (= UCMP V-5375), is not possible owing to the greater curvature of the preacetabular region and the greater subacetabular expansion (Fig. 1).

The other elements could be referred to *Litoria*, to *Limnodynastes* or to *Australobatrachus ilius*, all of which occur in the Etadunna Formation localities (Tyler 1982b), and give some further indication of the hylid affinities of the material. The humeri resemble those of higher frogs in general but can be referred tentatively to the Hylidae on the basis of general shape, well defined epicondylar crests and lack of an extensive or protuberant olecranon scar, as well as a relatively deep fossa cubitus ventralis.

The condyles of the sacral vertebrae are similar to those of hylids in tending to be flattened and well separated on the midline and the cotyles are also somewhat dorsoventrally flattened as in that group. In leptodactylids the condyles and cotyles are not so flattened and the vertebrae tend to be more hourglass-shaped

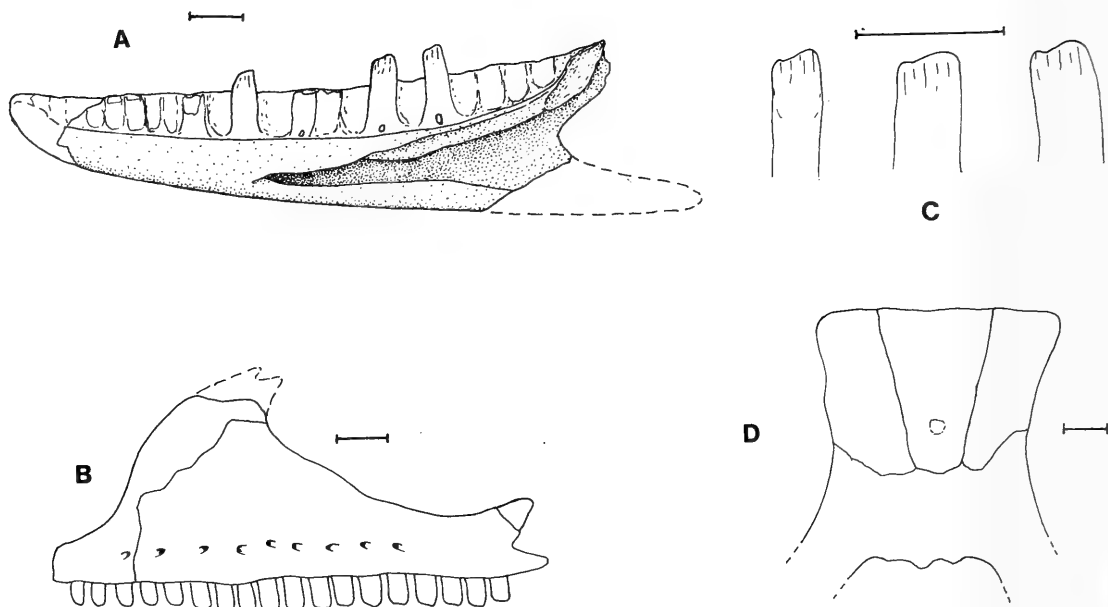


Fig. 1. A, *Litoria aurea* (Holocene, AMNH 64296, Albury, New South Wales, Australia), portion of left ilium, lateral view. B, *Australobatrachus ilius*, SAM P18021, holotype left ilium fragment, Miocene, Etadunna Formation, South Australia; from Tyler. C, *Litoria* sp., UCR 20811, fragment of right ilium (reversed for comparison), Miocene, Etadunna Formation, South Australia; dashed lines indicate restoration. Line = 1 mm. LIG = lateral ilial groove.

with the paired condyles closer together. As Tyler (1976) noted, distinguishing isolated elements of these two families is difficult and in addition the polarities of all these character states have not been determined. Other than the ilium, the fossils do not permit identification below the family level (indeed even the family allocation is difficult), but comparisons with other groups of Australian frogs, i.e. leptodactylids, microhylids and ranids, give no reason to suspect that these families are represented in the fossil sample. Hylids are common in Australia today and occur in northern North Australia, but no frogs have been recorded in the Lake Palankarinna area to present (M. Tyler, pers. comm. 1983).

Australasian hylids and leptodactylids have been separated as endemic families Pelodryadidae and Myobatrachidae, respectively, by some authors, but no morphological data that separate the groups are available and most authors have been reluctant to separate them solely on geographic grounds, as Savage (1973) has done. Tyler (1979; 1982a) pointed out that there was no basis for recognition

LOWER VERTEBRATES FROM THE ETADUNNA FORMATION

of either Pelodryadidae or Myobatrachidae; I have therefore retained the broader concept of these families here.

ORDER TESTUDINES

Family Chelidae

Material: A few UCR shell fragments. Gaffney (1979) identified the living chelid genus *Emydura* from UCMP locality V-5762 in the Etadunna Formation. The UCR specimens appear to be chelid but are not identifiable to genus.

Family Meiolaniidae

Gaffney (1981) identified skull and shell material of this family from UCMP locality V-5857 in the Etadunna Formation. No material referable to this taxon is available in the UCR collection.

ORDER SAURIA

Family Scinidae

Egernia sp.

Material: UCR 20814, dentary; 20815, parietal; 20816, maxilla; other unnumbered examples of these bones, as well as vertebrae and a fragmentary scapulocoracoid.

Comments: The dentaries have closely spaced, columnar teeth with chisel-shaped, striated crowns (Fig. 2C). The Meckelian groove is smoothly closed and fused (Fig. 2A). The maxillae have a prominent nasal process, a posterior process strongly forked at its tip, and a relatively blunt anterior process (Fig. 2B). There are about 23-24 dentary and 21-22 maxillary teeth. The parietal is subtriangular, with the supratemporal process missing. Dermal bone is present on the skull table, bearing the imprints of parietal and interparietal epidermal scales; the latter separates the paired parietal scales from each other (Fig. 2D). The vertebrae are procoelous with tapering centra.

While this material is rather scanty, several factors permit a fairly secure identification. The striated tooth crowns and closed Meckelian groove are also found in Gekkonidae, but these specimens, with their robust form and relatively few teeth, coupled with the strongly forked posterior process of the maxilla, are clearly referable to the Scincidae. The closed and fused Meckelian groove is a derived character state, and the extant Australian skinks that possess it are referable to the *Egernia* and *Eugongylus* groups (Greer 1979). The latter group is further derived in having contact of the parietal epidermal scales behind the interparietal scale, while the *Egernia* group maintains the primitive separation of the parietal scales. On the basis of the single derived state of closed and fused Meckelian groove, combined with the primitive parietal scale condition, the fossils are referred to *Egernia* sp., which had previously been reported from the Pleistocene of South Australia (Williams 1980). *Tiliqua* and *Corucia*, the other *Egernia*-group

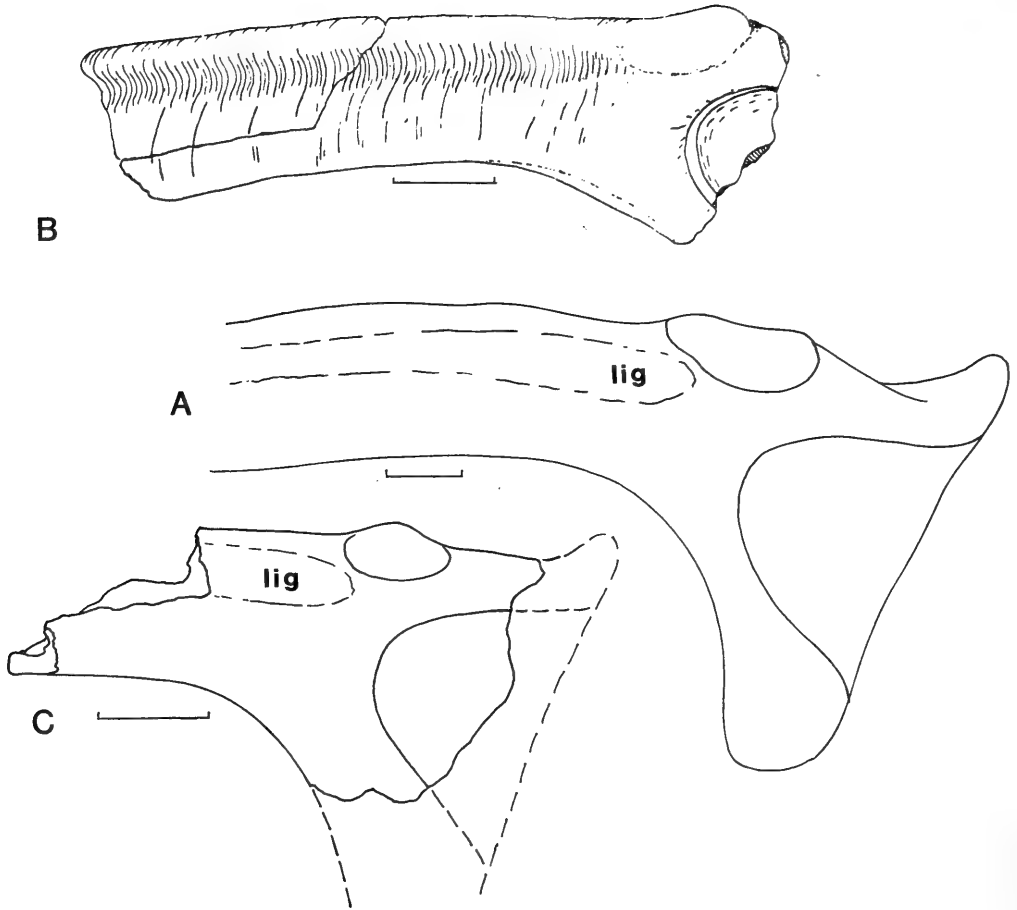


Fig. 2. *Egernia* sp., Etadunna Formation, South Australia. A, UCR 20814, dentary; restoration in solid line based on other specimens, dotted line based on extant examples. B, UCR 20816, maxilla; restoration as above. C, tooth crowns, showing striae; from left to right the three drawings represent anterior, middle and posterior teeth of a right dentary in labial view. D, UCR 20815, parietal; note parietal epidermal scale impressions are separated by a median interparietal. Line = 1 mm.

group genera, have enlarged molariform teeth that differ strongly from the columnar ones of *Egernia*.

The fossil parietal bones are very similar to those of a number of *Egernia* species, e.g. *E. whittii*, differing in having somewhat wider supratemporal processes. M. Hutchinson (pers. comm. 1981) has confirmed this similarity based on his collection, noting that the specimens are less like parietals of other species groups of *Egernia* in central Australia. In UCR 20815 the parietal foramen is filled with

bone, although its former position is clear, marked both by the different appearance of the bone filling the foramen as well as the presence of a depression both dorsally and ventrally; in another unnumbered specimen the foramen remains open.

The Holocene genus *Egernia* has many species and is widespread throughout Australia, with one species extending into New Guinea. Many *Egernia* spp. differ from each other only in minor color pattern or body scale differences (M. Hutchinson, pers. comm. 1981), and thus even a careful analysis of all species of *Egernia* might not permit species identification of this or even more complete material. The diverse habitat preferences of the various species do not permit any paleoecological conclusions. Recent biochemical work (Hutchinson 1981) confirms the generic groups used here but underscores the diversity found in species of *Egernia*.

Molnar (1982) listed no lizard fossils from the Etadunna Formation. Rich *et al.* (1982), however, listed "cf. spp. of *Egernia*" from the Ngama local fauna, which comes from Etadunna Formation localities slight younger (but presumably still middle Miocene) than those yielding the Nagapakaldi local fauna. The University of California (Berkeley) collections include other unpublished records of *Egernia* sp., as well as of the related genus *Tiliqua* (identified by Jacques Gauthier, pers. comm. 1984), these come from the middle Miocene Wipajiri Formation (Stirton *et al.* 1967), UCMP locality V-6213 (=RV-7231). Fossils from this locality are included in the Kutjamarpu local fauna, which is believed to be slightly younger than the Ngama local fauna (Rich, *et al.* 1982). The more definitive identification of *Egernia* in the present paper marks the earliest fossil record of the genus in Australia.

Family Varanidae

Varanus sp.

Comments: Stirton *et al.* (1961) incorrectly cited the presence of a "large but not gigantic" varanid lizard from the Etadunna Formation localities; the specimen is actually of a snake. Molnar (1982) did not record the presence of this genus in any of the Australian Miocene localities. There is, however, additional material of smaller varanids from the University of California (Berkeley) localities producing the Ngapakaldi fauna. These include *Varanus* vertebrae in the Berkeley collection, some of which show similarities to *Megalania*, the giant Pleistocene varanid from Australia (J. Gauthier, pers. comm. 1981); none of the specimens are referable to the latter genus, however (M. Hecht, pers. comm. 1981). At least two species of *Varanus* occur in the Lake Palankarina area today (Houston 1979), and this marks the first correctly identified Miocene record and the earliest occurrence of the genus in Australia.

ORDER CROCODYLIA

Comments: A few small, unidentifiable crocodilian teeth occur in the present sample; specimens from this site were also reported by Stirton *et al.* (1961). Crocodilians today are limited to the northern coastal region of Australia.

CONCLUSIONS

In summary, the identifiable lungfish, frog and lizard fossils from the Middle Miocene of Australia can be referred to genera still present there.

The lungfish *Neoceratodus* has often been found fossil in the Australian interior. The teleost families Percichthyidae and Ariidae are marine groups with freshwater relatives, but have no prior fossil record in Australia, according to Long (1982). The former group occurs in river drainages near the Etadunna Formation fossil sites today, but the Ariidae is not now present in the Lake Palankarinna area, being found in northern river systems more than 1,600 km from the fossil site.

The speciose hyloid frog genus *Litoria* occurs widely in Australia today but has not been recorded in the Lake Palankarinna area. At least three hylids are now known from Etadunna Formation localities (Tyler 1982a).

Crocodylians occur today only on the northern coastal region of Australia, but have often been reported as fossils in other parts of the continent.

The lizards *Egernia* and *Varanus* occur near the Etadunna Formation localities today, and the specimens described here are the earliest records of these genera in Australia. Recent studies by Jacques Gauthier on the University of California. (Berkeley) collections have further increased the known diversity of the Middle Miocene lizard fauna of Australia. He has identified *Tiliqua* sp. and an acrodont lizard (presumably an agamid) from localities in the Wipajiri Formation, which overlies the Etadunna Formation on the east side of Lake Ngapakaldi, South Australia.

So far as the present limited paleontological sample is concerned, the included taxa indicate a characteristically Australian ichthyofauna and herpetofauna in the Middle Miocene of South Australia, although one that was evidently much more widely distributed in the past.

ACKNOWLEDGEMENTS

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A New Miocene Vertebrate Faunal Assemblage from the Lake Eyre Basin: A Preliminary Report

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ABSTRACT

A new fossil locality at Mammalon Hill, Lake Palankarinna, occurs in Etadunna Formation-like sediments of younger age than in the type section, preserved in a small down-faulted area. Pollen analysis of carbonaceous sapropelic shales just below the fossil horizon suggests an age between mid-Miocene and mid-Pliocene, younger than previous Etadunna Formation pollen determinations. Closer definition is not possible, because of the paucity of the pollen flora and the lack of comparative pollen stratigraphy for this period.

Fossil vertebrates are rare but diverse, including representatives of seven bird families, and the following marsupials: a burramyid; a petaurid cf. *Pseudocheirus* sp.; *Ektopodon* n. sp.; at least two macropodoids *incertae sedis*; and a diprotodontid cf. *Neohelos* sp. The marsupials indicate an age between that of the Ngapakaldi local fauna and the Kutjamarpu local fauna. Although sparse, the evidence is enough to indicate a new distinct local fauna, to be called the Ngama local fauna.

INTRODUCTION

The first recognized Australian Tertiary vertebrate faunas in terrestrial sediments were found in the Lake Eyre Basin in 1953 as the result of the late Prof. R. A. Stirton's first expedition to Australia (Stirton 1954). (I am excluding the Pliocene Chinchilla fauna, which at that time generally was regarded to be Pleistocene in age.) The mammals that Stirton found were quite different from those of the well-known Pleistocene faunas.

Continuing work on successive expeditions greatly increased our knowledge of the Tertiary vertebrate faunas, so that in 1968 Stirton was able to publish, posthumously a summary of all known Australian vertebrate fossil-bearing Tertiary deposits (Stirton, *et al.* 1968). The 1970's saw Australian-based workers gradually taking over from Stirton's students, or those students becoming Australian-based.

Lake Palankarinna was the locality of the first Tertiary mammal to be discovered in mainland Australian non-marine sediments (Stirton 1954, 1955; Stirton *et al.* 1961). The sediments are gently down-warped into a broad syncline. However, it had been noticed by Tedford, Woodburne and others (e.g. Woodburne,

unpubl. field notes 15 Nov. 1972; Tedford, pers. comm., 24 Nov. 1976) that a structural and sedimentological complication occurred near the Lawson-Daily Quarry, UCMP V5769. North of this site stands a small hill connected by a saddle to the main cliff exposures and capped with red Tirari Formation (Stirton *et al.* 1961). Standing near the northern end of the Lake (Fig. 1), this hill was given the unofficial name "Mammalon Hill" by Stirton, who noticed fish and reptile bone scraps on the surface of the connecting saddle. However, it was not until 1976, during an unofficial excursion following the 25th International Geological Congress, that the author found the first mammal fossil at this site.

This specimen proved to represent a new species (Pledge, in press), of the enigmatic marsupial *Ektopodon*, different from *E. serratus* (Stirton *et al.* 1967) from the younger Wipajiri Formation, and another species from lower in the Etadunna Formation. Subsequent work to clarify the stratigraphic setting and obtain more specimens of *Ektopodon* produced a variety of fossil vertebrates.

The system of tooth numbers used in this paper follows the nomenclature of Archer (1978).

GEOLOGICAL SETTING

The beds of Lake Palankarinna display a sequence from a probable early Tertiary basement (the Eyre Formation, *vide* Wopfner *et al.* 1974), through the Etadunna Formation to the overlying gypsiferous red silts and sands of the Plio-Pleistocene Tirari Formation. Intercalated with these are the Mampuwordu Sands: pre-Tirari channel deposits cut into the underlying Etadunna Formation, and the Katipiri Sands: channel deposits within the Tirari Formation (Stirton *et al.* 1961).

The Etadunna Formation in the type section at Lake Palankarinna is a sequence of alternating grey-green silts and clays with minor sand lenses, and an extensive, massive, white dolomite and calcareous mudstone near the exposed base. A minor white calcareous mudstone unit occurs higher in the sequence in the central part of the exposures. With the undulations of the beds, the main dolomite is best exposed at the southern end of the lake, but it gradually dips beneath alluvial cover and disappears about one-third of the way north along the lake. It suddenly reappears at the northern end of the lake, presumably because of a vertical, east-west striking fault contact, best seen in the cliff face 70 m north of Mammalon Hill. This contact is interpreted as a minor fault of unknown vertical displacement. Hand augering to about 2 m failed to intersect equivalent units on either side of the fault.

To the north of the contact, the sediments are identical in aspect with those at the southern end of the lake. The prominent white unit, so obvious even from a distance, I tentatively correlate with the upper part of the main dolomitic limestone, unit 2(e) of Stirton *et al.* (1961), although it is much thinner than in the type section. Immediately south of the fault, the sediments are superficially the

MIOCENE FAUNAL ASSEMBLAGE FROM LAKE EYRE BASIN

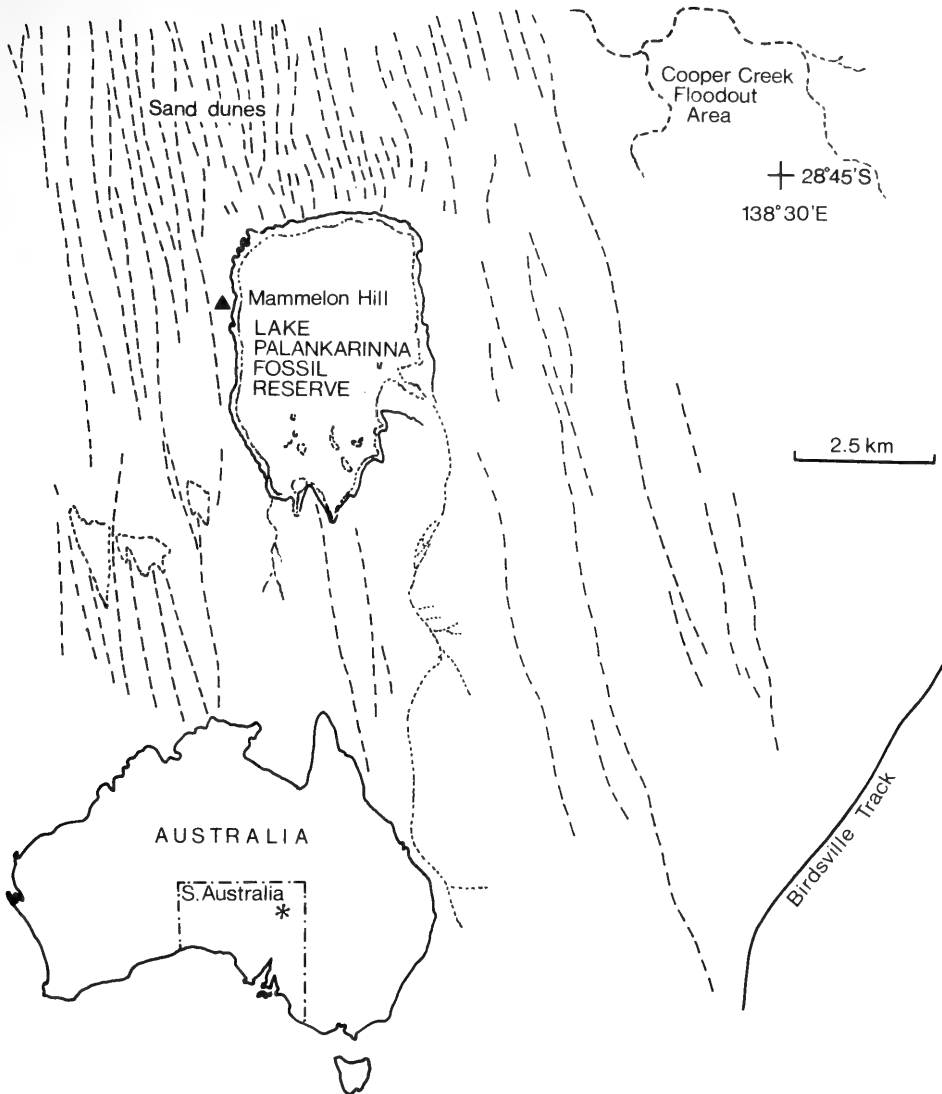


Fig. 1. Locality map, Lake Palankarinna, South Australia.

same, except for the absence of the white dolomite and the presence of a dark-grey to black clay-stone near the top and a brown waxy, carbonaceous shale at the base of the exposed sequence (Fig. 2).

On the south-eastern half of Mammelon Hill there is a large stream channel deposit, predominantly of fine, friable, white to pale grey, silty sand. This cuts

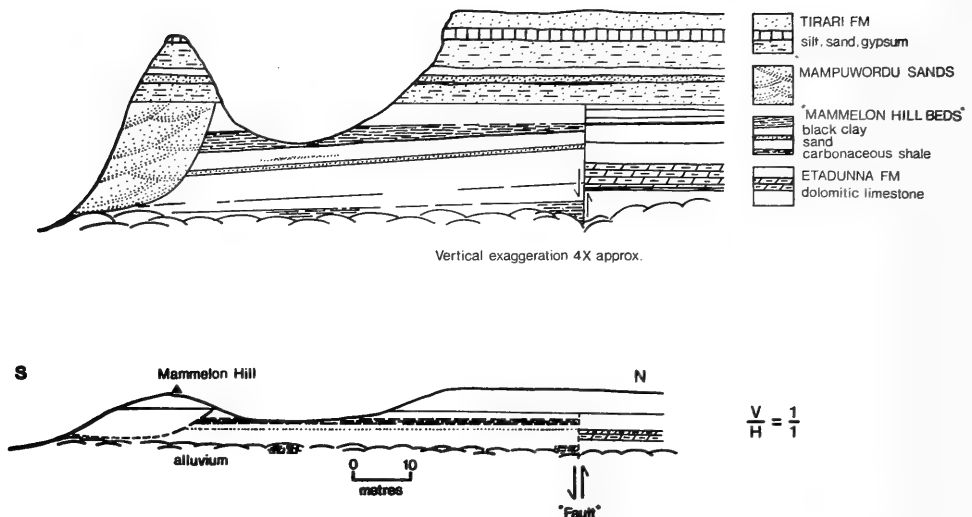


Fig. 2. Geological profile at Mammelon Hill, Lake Palankarinna.

down through the black and greenish grey claystones and silts, but not as deeply as the carbonaceous shale. Although no fossils have been found in this channel deposit, it is correlated with the Mampuwordu Sands, which formed the fossiliferous unit of the Lawson-Daily quarry, UCMP V5769, several hundred metres to the south.

The *Ektopodon* sp. discovery was made on the surface of the grey beds just below the distinctive black claystone, in the saddle between Mammelon Hill and the main cliff.

TYPE LOCALITY

The type locality for the new fossil assemblage is Mammelon Hill, on the northwestern shore of Lake Palankarinna, at Grid Reference 656432 on the 1:250000 Kopperamanna map sheet (Australian R502 map series, SH/54-1), latitude 28°45'50"S, longitude 138°24'E. (See Fig. 1).

The new Ngama local faunal assemblage comes from sandy layers below the saddle connecting Mammelon Hill to the main cliff. Careful excavation and screen-washing of these horizons, one of which produced the *Ektopodon* sp. jaw in 1976, have yielded more mammalian fossils of sufficient variety and distinctiveness to warrant a separate faunal name — Ngama Faunal Assemblage. This name uses a Dieri Aboriginal word meaning breast, in allusion to Mammelon Hill.

DETAILED STRATIGRAPHY

Four stratigraphic sections were measured at and adjacent to the fossil site in an attempt to place the fossils in a known stratigraphic context. These were:

TABLE 1. Stratigraphic sections, Mammalon Hill.

Section 1	Section 2	Section 3	Section 4
Tirari Fm. 3m red-brown silty sand with gypsum. Top not preserved.	Tirari Fm. 4.6m red-brown silty sand. Gypsite at top.	Tirari Fm. 4.5m red-brown silty sand with gypsite cap.	Tirari Fm. 4.5m red-brown silty sand with gypsite cap.
Mampuwordu Sands (?) 1.2m pale-grey silty sand	Etadunna Fm. (s.l.) 1.3m green-grey claystone, some gypsum, rare bone fragments on surface	Etadunna Fm. (s.l.) 1.2m light-grey claystone	Etadunna Fm. 1.1m light-grey claystone, silty at base
1.4m pale-grey silty sand with limonite mottling	1.0m dark-grey to black claystone	0.3m dark-grey to black claystone	0.9m green-grey claystone
0.9m clean, white, friable sand	1.0m green-grey claystone, limonitic; thin sandy partings near middle and base, with bone. (<i>Ektopodon</i> levels)	0.7m light-grey claystone with limonite	1.1m grey claystone, limonitic
Etadunna Fm. 0.45m grey silty clay	0.3m white sand with grey clay pellets	0.2m light-grey silty sand with bone chips	1.3m hard white massive dolomite dipping 10°NW
1.5m green-grey clay, with limonitic mottling	1.4m green-grey claystone, limonitic staining, siltier at middle and base	1.7m grey claystone, increasingly limonitic	0.15m loose brown sand
-----	0.45m purple-brown claystone	1.1m purple-brown carbonaceous claystone	1.1m light-grey claystone
alluvium	0.6m dark-brown carbonaceous shale - waxy	0.65m dark-brown carbonaceous clay	----- alluvium
	alluvium	alluvium	
Total: 8.45 m	10.65 m	10.35 m	10.15 m

(1) On Mammalon Hill itself, through the channel deposit; (2) from the cliff to the saddle and down through the fossil site; (3) one metre south of the fault contact; and (4) on the immediate north side of the fault. Measurement was done using a calibrated staff and a "Quicksite" surveyor's level. Results are summarised in Table 1. (See also Fig. 2).

There are two distinctive units exposed in the Mammalon Hill section. The lower-most one is a dark brown carbonaceous shale, so rich in remains of the alga *Botryococcus* that it approaches being an oil shale (W. K. Harris, pers. comm., 1980). Its thickness and lateral extent have not been determined.

The upper unit is a dark grey to black claystone, whose known extent is limited essentially to the saddle of Mammalon Hill and the cliffs as far north as the fault. It has been removed by erosion west and south of Mammalon Hill. Thin dark grey claystones of limited extent are known elsewhere at Lake Palankarinna, but are so minor and inconspicuous that they have been ignored previously, and there is no evidence at hand to equate them with the sediments at Mammalon Hill. Callen and Tedford (1976) reported black claystone as an important component of the lower part of the Namba Formation in the Tarkarooloo Basin, south-east of Lake Frome. The main constituent of that rock was the clay mineral smectite. Analysis of the Mammalon Hill black claystone failed to reveal smectite (AMDEL Report GS 1994/79), the main constituent being montmorillonite, a component common in the grey clays. The black coloration was considered to be due to a relatively high concentration of iron in the montmorillonite. Thus, the major change of depositional environment deduced for the Namba Formation (Callen & Tedford 1976) could not be applied to the Mammalon Hill area.

These two units are good markers in attempting to position the Mammalon Hill sediments. Neither has been stated to occur in the Etadunna Formation as defined by Stirton *et al.* (1961), and conversely, no distinctive marker bed from the standard Etadunna sequence can be seen at Mammalon Hill. Since the local base of the Etadunna formation can be seen in sequence at the south end of the lake, it must be concluded that the beds at Mammalon Hill are higher than those of the typical section. They have evidently been preserved and protected by local down-faulting of the sediments. The amount of displacement is unknown, but may be more than 19 m, assuming the dolomite on the north side of the fault is Stirton's unit 1(e). The fault extends due west, and can be traced about 100 m by marking the abrupt cut-off of the outcrops of white dolomite. Alternative suggestions that the Mammalon Hill sediments are older than the typical Etadunna Formation and exposed by uplift of the fault block, or are deposited in an eroded basin (with sheer walls), are not supported by the evidence.

AGE

No surface sample of the Etadunna Formation has produced spores or pollen, and the age of these superficial beds has been determined by correlation with the

MIOCENE FAUNAL ASSEMBLAGE FROM LAKE EYRE BASIN

lower part of similar sediments in the Lake Eyre No. 20 bore, where pollens indicating an early to middle Miocene age have been found (Balme 1963, Callen & Tedford 1976). W. K. Harris has recently analysed samples of the carbonaceous shale from Mammalon Hill. The microflora contained therein is depauperate of pollen species, but rich in the alga *Botryococcus*, with subordinate *Pediastrum*. The pollens and spores that are present indicate *Casuarina* sp. (as *Haloragacidites harrissi*), *Acacia* sp., *Dacrydium* sp. (as *Lygistepollenites florinii*), a restionacean (as *Milfordia* sp.), sparganiacean or typhacean (as *Sparganiaceae-pollenites* sp.), and a fern *Gleichenia* sp. (W. K. Harris, pers. comm., 18 March 1980; Trusswell & Harris 1982). This assemblage, together with the lithology, suggests a billabong or ox-bow environment. No *Nothofagus* pollen has been found in this horizon, suggesting that it is younger than the assemblage at the base of the Etadunna Formation (Balme 1963). The microflora seems to fall into a time zone where there is little comparative material from elsewhere in Australia. Thus, the age suggested by palynology is between Middle Miocene and Middle Pliocene (Harris, pers. comm.) — a span of possibly 10 million years. Evidence deduced by comparison of the mammals in this and other deposits suggests the older age, but one certainly younger than that of the typical Etadunna Formation.

NGAMA LOCAL FAUNAL ASSEMBLAGE

A variety of vertebrate fossils, representing fish, reptiles, birds and mammals has been collected from the Mammalon Hill beds.

The fish and reptile remains, which occur in relative abundance, are not noticeably any different from those in the lower Etadunna Formation, for which Estes (1980, 1984) produced a provisional systematic list, Gaffney (1979) has also studied the turtles from the Etadunna Formation. Drs P. V. Rich and G. F. van Tets (pers. comm., 1980, 1981; and Rich & van Tets 1982) have made preliminary identifications of eight bird bones collected as float around the site. Another (a burhinid coracoid, SAM P. 23625) was excavated from the upper sand horizon, as was an emu leg bone (SAM P. 23977).

OSTEICHTHYES

Dipnoi

Neoceratodus sp. — lungfish (primarily teeth)

Teleostei (spines, vertebrae, and skull elements)

Ariidae

Percichthyidae

REPTILIA

Chelonia

cf. *Emydura* sp. — turtles (carapace plates)

Crocodylia

Crocodylus sp. — crocodiles (teeth)

Squamata

Scincidae

Egernia sp. — a lizard (dentary)

AVES

Casuariidae — an emu (tarsometatarsus)

cf. Anatidae — probably a duck (scapula, ulna, humerus fragment)

Rallidae — a small rail (tibiotarsus fragment)

cf. Burhinidae — a stone curlew (humerus fragment, coracoid)

Charadriiformes — small wader (humerus fragment)

Phoenicopteriformes — a flamingo (tibiotarsus fragment)

Columbidae — a pigeon (humerus)

cf. Accipitridae — a hawk (coracoid)

MAMMALIA

Marsupialia

Burramyidae — a pygmy possum (one molar)

Petauridae

cf. *Pseudocheirus* sp. — a ringtail (several teeth)

Ektopodontidae

Ektopodon sp. (mandible, several isolated teeth)

Macropodoidea, genera *incertae sedis* — small wallabies (partial skeleton without teeth, isolated maxilla, dentary, incisor, premolars, molars, ankle bones).

Diprotodontidae

cf. *Neobelos* sp. — a quadrupedal herbivore (limb bones, tooth fragments)

COMMENTS

Obviously, more material is needed before definitive statements can be made about most of these species. Nevertheless, a few comments about the mammals are warranted.

Pseudocheirine petaurids are represented by three well-preserved teeth, a right M^4 , left M^2 and left P^3 which seemingly represent the same species, one very close to *Pseudocheirus peregrinus* in size and morphology. A fragment of humerus may also relate to this taxon.

Ektopodon sp. nov. is represented by a jaw bearing a well-preserved premolar and first molar, and the following two molars, which are incomplete. The last molar, M_5 , is missing. A perfect first upper molar, M^2 , a good M^3 and fragments of another two molars were found separately. Also present are several unusual teeth considered to be upper incisors of *Ektopodon* sp. nov.

This species is considered (Pledge) to be morphologically intermediate between the younger genotype *E. serratus* (Stirton *et al.* 1967) and a new genus and species (Woodburne & Clemens 1984) from lower in the Etadunna Formation. I consider the Mammalon Hill material to be morphologically more specialized than representatives of the same species found at Lake Tarkarooloo (Pledge 1984).

MIOCENE FAUNAL ASSEMBLAGE FROM LAKE EYRE BASIN

The fossils listed under the heading Macropodoidea comprise at least two species in two families. The first-found specimen, a lower molar, may represent the same macropodoid species as the maxilla (SAM P. 23990). The isolated pre-molars were initially compared with those of *Aepyprymnus*, but seem to match molars removed from the crypt in a mandible (SAM P. 23626). This specimen is similar in size and form to the mandible of *Aepyprymnus rufescens* (e.g. SAM M. 2753, ♀), although the ascending ramus is more vertical. However, the molars are lophodont and about the size of those of *Bettongia gaimardii* (SAM M. 7386, ♂). The mandible is considered (T. Flannery, pers. comm., 17 Dec., 1982) to represent a potoroid related to *Wabularoo* (Archer 1979), a taxon incorporating both potoroid and macropodid features.

In view of the presence of several species based on dental criteria, it is not possible to ascribe positively the partial skeleton and other isolated bones. The skeleton has not yet been completely examined, but is notable for the relatively long forelimbs. The limb-bone proportions are similar to those of the primitive musk rat-kangaroo *Hypsiprymnodon moschatus* and the bandicoot *Macrotis lagotis*, and quite different to those of the typical kangaroos and rat-kangaroos. Apart from their smaller size, the isolated ankle bones appear similar to those of the skeleton, which may represent the potoroid.

A small collection of isolated and fragmentary diprotodontid fossils is referred to the genus *Neobelos*, based on a deciduous and a permanent molar, both well-preserved. Other material includes two incisors, two partial humeri, and an astragalus. Species of *Neobelos* are known from the Kutjamarpu local fauna (Stirton *et al.* 1967) and the younger Bullock Creek local fauna (Plane & Gatehouse 1968, Stirton *et al.* 1968). M. D. Plane (pers. comm., 1978) suggested this material might represent a new and smaller member of the genus.

DISCUSSION

As noted above, the *Ektopodon* species in the Ngama assemblage is considered to be morphologically intermediate between taxa from the Ngapakaldi local fauna and the younger Kutjamarpu local fauna. It is somewhat closer in form to the latter. Elsewhere (Pledge 1984) I have indicated that a variant of *Ektopodon* from the Tarkarooloo local fauna at Lake Tarkarooloo (Rich & Archer 1979) in the Lake Frome area is somewhat less specialized. At that site, the species occurs with *Ngapakaldia tedfordi* (Rich & Rich 1982). At Mammalon Hill, it occurs with a species similar to *Neobelos* spp., while in the Kutjamarpu local fauna, *Ektopodon serratus* occurs with the larger *Neobelos tirarensis* (Stirton *et al.* 1967).

Thus, the Ngama local fauna of Mammalon Hill would be separated by an appreciable time gap from the underlying Ngapakaldi local fauna, which is apparently older than the Tarkarooloo local fauna. There is possibly a smaller time separation from the younger Kutjamarpu local fauna.

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Mrs Joan Murphy typed the manuscript. Jenni Thurmer drew the figures.

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The Macropodoids (Marsupialia) of the early Pliocene Bow Local Fauna, Central Eastern New South Wales

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ABSTRACT

Sixteen kinds of macropodoids, including macropodines, sthenurines, potorines and hypsiprymnodontines, can be recognised in the early Pliocene Bow local fauna of the Hunter Valley in central eastern New South Wales. Of these, seven can be identified to species (*Propleopus* n. sp., *Troposodon bowensis* Flannery and Archer, 1983, *Kurrabi mahoneyi* n. sp., *Kurrabi merriwaensis* n. sp., *Protemnodon chinchillaensis* Bartholomai, 1973, *Macropus dryas* DeVis, 1895 and *Macropus (Osphranter) pavana* Bartholomai, 1978) a further two or three confidently to genus (*Simosthenurus* sp. and *Troposodon* sp., one or two species).

The majority of Bow macropodids possess moderately hypsodont molars, often with elongate, trenchant premolars. This suggests a woodland and/or savanna environment. There are, however, a few Bow species with brachydont molars (i.e., cf. *Dendrolagus* spp. that may have been derived from a rainforest habitat. The closest affinities of the Bow kangaroos seem to lie with kangaroos from the early Pliocene Hamilton and Bluff Downs local faunas and, more distantly, with those of the early to middle Pliocene Chinchilla local fauna. Thus, Skilbeck's (1980) preliminary assessment of the age of the Bow local fauna as early Pliocene (4-4.5mybp) is supported.

INTRODUCTION

A preliminary report by Skilbeck (1980) describes the geology and fossil fauna of the Bow locality of the Hunter Valley, New South Wales. The fossils occur in fluvial sediments exposed in a road cutting. Bones from the locality are most often fragmented and almost never associated (an exception may be the holotype and a referred specimen of *Kurrabi mahoneyi* n. sp.). Skilbeck suggests that the site represents an ephemeral gully facies. At the time of Skilbeck's review, only six species of Bow macropodoids were recognised: *Propleopus* sp.; *Macropus (Osphranter)* sp. cf. *M. (O.) woodsi* (here recognised as *M. (O.) pavana*); *Protemnodon chinchillaensis*; *Troposodon* sp. cf. *T. bluffsensis* (later described by Flannery and Archer 1983 as *T. bowensis*); *Sthenurus* sp. (here recognised as *Simosthenurus* sp.); and an unnamed genus (here recognised as a new macropodine genus, *Kurrabi*, containing two new species, *K. mahoneyi* and *K. merriwaensis*). Skilbeck (1980) also noted the presence of gastropods, bivalves, crustaceans, chelonians, *Dasyurus* sp., *Phascolonus* sp., *Thylacoleo crassidentatus*, *Palorchestes* sp. cf. *P. parvus* and a nototheriine. Subsequently, Archer (1982)

recognised *Dasyurus dunmalli* (*Dasyurus* sp. of Skillebekk), and Archer and Dawson (1982) recognised *Thylacaleo* sp. cf. *T. hilli* in the Bow local fauna.

Dental homology and terminology follows Archer (1976, 1978). AM F is a prefix for fossil specimens held in the Australian Museum (Sydney). The registration numbers of all macropodoid dental fragments from Bow not mentioned in the text or in other publications are given in Appendix 1. Pledge (1980) is followed in recognising *Shenurus* and *Simosthenurus* as separate genera.

SYSTEMATICS

SUPERFAMILY MACROPODOIDEA (GRAY, 1821)

FAMILY POTOROIDAE GRAY, 1821

SUBFAMILY HYPSPRYMNODONTINAE COLLETT, 1887

Propleopus Longman, 1924

Propleopus sp.

A new species of *Propleopus* from the Bow local fauna, represented by a dentary, is presently being described by W. D. L. Ride and J. A. Mahoney (J. Mahoney pers. comm.).

SUBFAMILY POTOROINAE (GRAY, 1821)

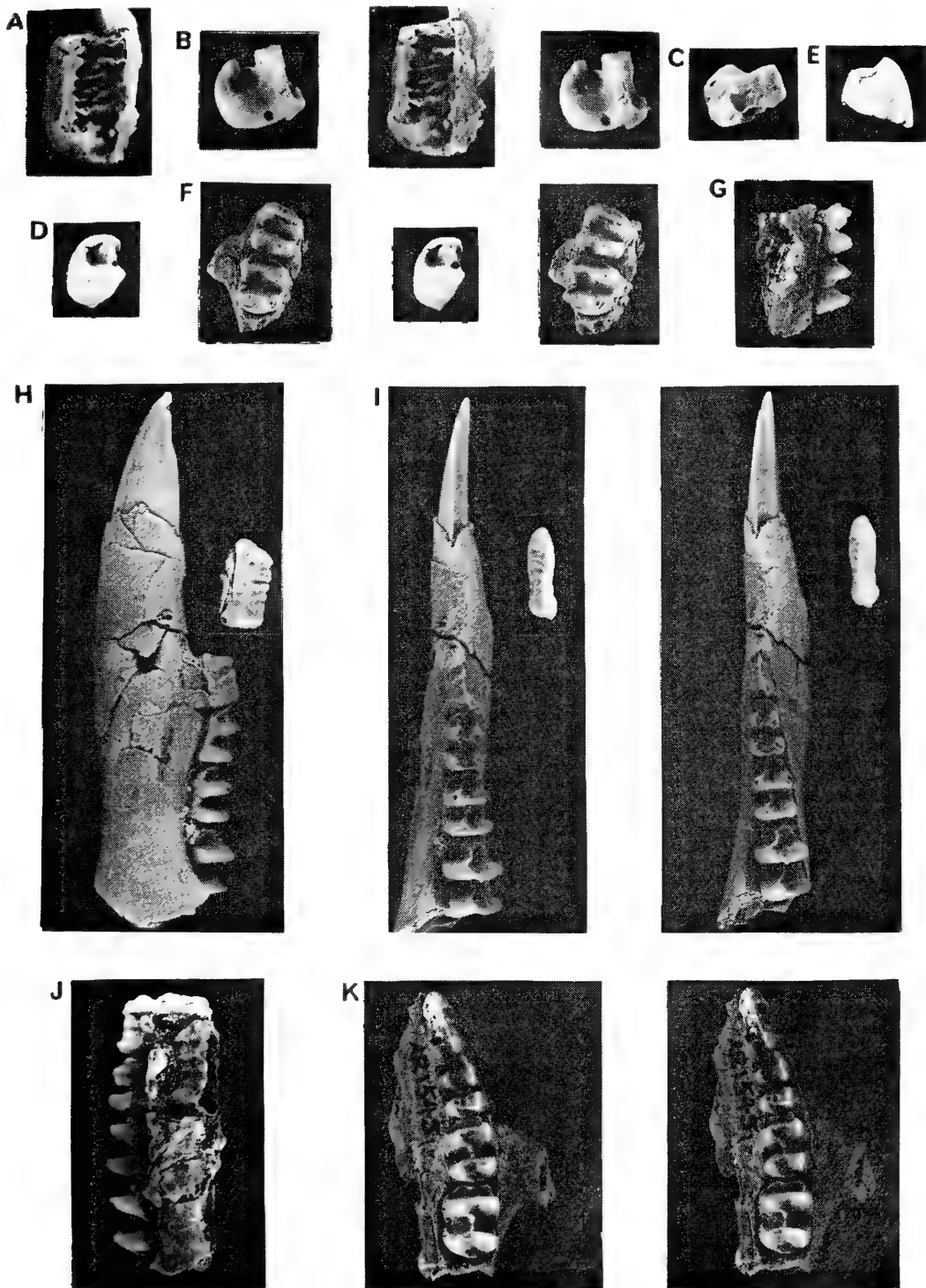
Genus indet.

(Figure 1D,E)

Material. A single molar fragment from Bow, AM F64003, probably the hypoloph of a right M⁴, represents a potoroine.

Description. The tooth fragment is relatively high-crowned and its lingual margin slopes at a low angle to the base of the crown relative to that seen in most other potoroids. The pre- and posthypocristae are strongly-developed, the latter forming a continuous posterior cingulum by joining the postmetacrista. There is a slight premetacrista. The hypoloph is weakly-developed.

Fig. 1. A, stereopair of occlusal view of AM F64002, right P³ fragment of *Simosthenurus* sp., X2. B, stereopair of occlusal view of AM F64004, posterior portion of right P₃ of *Dendrolagus* sp., X2. C, lingual view of same specimen, X2. D, stereopair of occlusal view of AM F64003, hypoloph of right M⁴ of a potoroine, X2. E, posterior view of same specimen, X2. F, stereopair of occlusal view of AM F64007, M³⁻⁴ of cf. *Dendrolagus*, X1. G, lingual view of same specimen, X1. H, lingual view of holotype of *Kurrabi mahoneyi* (AM 64016), left dentary containing P₂, P₃ (removed from crypt), M₁₋₃, X1. I, stereopair of occlusal view of the same specimen, X1. J, lingual view of AM F64020, juvenile left maxillary fragment containing P², P³ (in crypt), M¹⁻³ of *Kurrabi mahoneyi*, X1. K, stereopair of occlusal view of same specimen, X1.



Discussion. This fragment resembles upper molars of an unnamed genus of potorine of the Hamilton local fauna in being high-crowned and in possessing lingual upper molar margins that slope at a low angle to the base of the crown (Flannery *et al.* in prep.). However, the Bow specimen is smaller than the Hamilton form and, on the basis of this evidence alone, the two are probably not conspecific. In being high-crowned, the Bow specimen also resembles *Aepyprymnus rufescens*. It differs from *A. rufescens*, however, in lacking the extremely well-developed posthypocrista that forms most of the posterior cingulum of the upper molars of the latter species.

FAMILY MACROPODIDAE GRAY, 1821
SUBFAMILY STHENURINAE (GLAUERT, 1926)
Simosthenurus Tedford, 1967
Simosthenurus sp.
(Figure 1A)

Material. A species of *Simosthenurus* is represented in the Bow local fauna by two specimens, a P³ fragment (AM F64002) and a lower molar (AM F60670).

Diagnostic features. These specimens have been assigned to the genus *Simosthenurus* for the following reasons. Only species of *Sthenurus*, *Simosthenurus* and *Procoptodon* among macropodoids possess a P³ with a very high lingual cingulum and with many tall enamel ridgelets in the valley between the main blade and the lingual cingulum. These characteristics are seen in the Bow premolar fragment (see Fig. 1A). The molars of the species of *Sthenurus* are higher-crowned and have less crenulate enamel than the Bow specimen, while the molars of the species of *Procoptodon* are higher-crowned and often possess fissures in the hypolophid, characteristics that the Bow premolar lacks. The molars of species of *Simosthenurus* resemble the Bow molar in being low-crowned and in possessing crenulate enamel.

Description. Unfortunately, the *Simosthenurus* molar from Bow can no longer be located. The premolar fragment consists of the posterolingual moiety of the tooth (see Fig. 1A). The low posterolingual cusp does not join directly to the main crest. The lingual cingulum, although high, is noticeably lower than the main crest, the full height of which may not be preserved. The valley between the lingual cingulum and the main crest is broad and is crossed by many anastomosing enamel ridgelets.

Discussion. The Bow P³ fragment differs from the single known P³ of *Simosthenurus antiquus* (the only Pliocene *Simosthenurus* named so far) in the following ways: The posterior-most part of the valley separating the main crest and the lingual cingulum is ornamented with anastomosing ridges rather than longitudinally oriented striae such as occur in *S. antiquus* where the more anterior part of the valley is filled with many more, higher anastomosing ridgelets. The P³ of *Sthenurus notabilis* (the only Pliocene species of *Sthenurus*) is not known.

Troposodon Bartholomai, 1967

Troposodon bowensis Flannery and Archer, 1983

Flannery and Archer (1983) noted the presence of two or three species of *Troposodon* in the Bow local fauna. A small primitive species, *Troposodon bowensis*, is the most abundant marsupial at the site.

Troposodon spp.

Several *Troposodon* specimens found at the Bow locality are from larger species than *T. bowensis*. They may represent extreme variants of *T. minor* or one or two unnamed forms (Flannery and Archer 1983).

SUBFAMILY MACROPODINAE (GRAY, 1821)

Dendrolagus Muller, 1839

cf. *Dendrolagus* sp. 1

(Figure 1B,C)

Material. The posterior fragment of a right P³, AM F64004, may represent a small species of *Dendrolagus* at Bow.

Diagnostic features. This specimen is tentatively assigned to the genus *Dendrolagus* because, apart from species of *Sthenurus*, *Simosthenurus* and *Procoptodon*, the species of *Dendrolagus* are the only macropodoids known to develop a postero-buccal cusp on P³. Species of *Dendrolagus* can be distinguished from species of the above three sthenurine genera by being much smaller, possessing a lower lingual cingulum on P³, and in having the valley between the main crest and the lingual cingulum with far fewer (and much weaker) enamel ridgelets.

Description. The P³ fragment consists of the posterior portion of the main blade. lingual cingulum and a postero-buccal and posterolingual cusp. A single small cuspule and associated groove are preserved on the remaining portion of the straight main blade anterior to the large posterior cusp. The postero-buccal cusp is situated at the posterior end of the tooth. It is two-thirds the height of the main blade and is fused to it for its entire height. The posterolingual cusp is broad and blade-like. Between it and the main blade, posteriorly, there is a small but deep circular posterior fossette. The posterolingual cusp merges into the lingual cingulum to form a broad sweeping crest that converges on the main blade anteriorly to the point at which the tooth is broken away (see Fig. 1B,C).

Discussion. This tooth fragment closely resembles P³ fragments assigned to cf. *Dendrolagus* sp. from the Hamilton local fauna (Flannery *et al.* in prep.). It differs from the Hamilton specimens in being more worn, slightly larger and in having the posterolingual cusp more continuous with the lingual cingulum. All of these fragments most closely resemble the P³ of *Dendrolagus bennettianus* among living tree kangaroos. They differ, however, in being much smaller and in having a relatively smaller postero-buccal cusp (see Table 1). On the basis of their extremely fragmentary remains, the Hamilton and Bow specimens of cf. *Dendrolagus* may be conspecific.

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TABLE 1. Dental measurements for some species of macropodids from the Bow local fauna. All measurements are in mm. L = length, AW = anterior width, PW = posterior width.

			L	AW	PW
Potorinae indet	F 64003	M ⁴			5.2
cf. <i>Dendrolagus</i> sp. 1	F 64004	P ³			6.2
cf. <i>Dendrolagus</i> sp. 2	F 64007	M ³	7.8	6.7	6.5
		M ⁴	8.5	6.8	6.5
<i>Protemnodon chinchillaensis</i>	F 59533	P ³	18.8	7.8	9.3
		M ²	10.2	10.3	10.6
		M ³	12.0	11.1	10.6
	F 59530	M ²	10.6	10.3	10.4
		M ³	12.2	11.1	11.0
		M ⁴	13.2	11.5	10.5
		M ⁵	13.3	10.9	8.7
	F 59606	M ³	11.0		
		M ⁴	12.5		
	F 64034	P ₃	16.0	7.0	6.3
		M ₃	11.6		
		M ₄	13.8	10.8	10.7
		M ₅	14.8	10.8	9.7
	F 59537	M ₃	13.7	9.4	9.0
	F 59549	M ₂	12.3		8.2
<i>Macropus dryas</i>	F 59535	P ²	7.9	4.2	5.1
		P ³	12.2	3.8	5.7
		M ¹	8.3	6.0	6.2
		M ²	8.7	7.0	7.0
		M ³	10.5	7.9	7.5
	F 64065	M ²	9.4	7.2	7.6
	F 64064	M ³	10.4	8.4	7.8
	F 59546	M ₂	8.1		6.1
		M ₃	11.5	7.1	7.3
		M ₄			8.2
<i>Macropus (Osphranter) pavana</i>	F 59532	M ³	11.3	9.8	
		M ⁴	12.8	10.4	9.9
	F 59536	M ⁴	13.6	10.2	
		M ⁵	14.6	11.4	10.6
	F 59573	P ₃	9.6		
		M ₁	10.2		
	F 64033	P ₃	8.8	3.4	4.7
		M ₁	9.6	5.5	11.7
		M ₂	11.1	7.3	7.8
		M ₃	12.4	8.4	8.1
	F 59534	P ₃	8.8	3.6	4.7
		M ₃	14.0		
	F 59548	M ₃	11.0		
		M ₄	15.2	9.0	9.0
<i>Macropus (Osphranter) pavana</i>	F 59585	M ₃	13.0	8.4	
		M ₄		9.3	
		M ₅			8.0
	F 64055	M ₅	15.4	9.6	8.6
Macropodinae Indet.1	F 64001	M ₄	9.5		
Macropodinae Indet.2	F 64008	M ²		4.0	
	F 64010	molars			4.0
	F 64009	lower			3.4

cf. *Dendrolagus* sp. 2

(Figure 1F,G)

Material. A maxillary fragment containing M^{3-4} (AM F64007) and an isolated M^5 (AM F59576) are probably referable to a large *Dendrolagus*-like animal.

Diagnostic features. These molars clearly belong to a brachydont, primitive macropodine and are very similar to those of some species of *Dendrolagus*. They are too large to belong with the previously described premolar fragment tentatively assigned to *Dendrolagus*. While superficially resembling the molars of the species of *Dorcopsis*, they differ in lacking a forelink, in having a much weaker postparacrista and premetacrista, in having slightly broader interloph valleys and in being slightly more elongate. They are similar in size to the molars of a maxillary fragment referred by Plane (1967) to *Dorcopsis* sp. from the Pliocene Awe local fauna of New Guinea, from which they differ mainly in having weaker postparacristae and premetacristae. This same characteristic and superior size distinguish the Bow fossils from *Dendrolagus dorianus* and *D. goodfellowi*. Apart from their superior size, they most closely resemble the upper molars of *D. bennettianus* and *D. lumboltzi*. Because *Bohra paulae* Flannery and Szalay, 1982, a gigantic primitive tree-kangaroo from Pleistocene deposits in Wellington Caves, New South Wales, is known only from postcranial remains, these two forms cannot be compared. However, both are of large size and primitive morphology.

Description. The maxillary fragment is poorly-preserved. The base of the masseteric process can be distinguished but its size cannot be determined. It is situated above the anterior end of M^4 . A part of the alveolus of the posterior root of M^2 and of the anterior root of M^5 are preserved.

The M^3 is only slightly-worn and is low-crowned. The hypoloph and protoloph are subequal in width. The anterior cingulum extends across the width of the tooth. A moderately strong preparacrista connects the paracone to the lingual side of the anterior cingulum. There is no forelink and the midlink is very poorly-developed. The interloph valley is shallow but with a narrow base. There is a strong postparacrista, premetacrista and posthypocrista, but a weaker postmetacrista. The posthypocrista swings buccally to join the almost vertical postmetacrista. The M^4 differs from M^3 in the following ways: it is larger; a slight postprotocrista runs to join the midlink near the centre of the posterior of the protoloph; the posthypocrista is less well-developed. The M^5 differs from M^4 in being broader and is obviously from a different individual. The hypoloph is narrower than the protoloph, and the interloph valley seems to be slightly broader than on M^4 (see Fig. 1F,G).

Discussion. This taxon is of little stratigraphic or taxonomic use at present as it is so poorly-known and does not match closely any named species. However it does provide further evidence for a brachydont macropodid element in the Bow local fauna.

Kurrabi n. gen.Type species: *Kurrabi mahoneyi* n. gen. and sp.

Generic diagnosis. Species of *Kurrabi* can be distinguished from other macropodoids as follows. They differ from potoroids (except bulungamayines) in possessing lophodont molars. They can be distinguished from bulungamayines by lacking highly bulbous, finely-grooved premolars, masseteric canal extending to below P^3 and a convex ventral margin of the dentary below the middle part of the molar row. They can be distinguished from sthenurines by lacking a prominent postlink on the upper molars and a well-developed premetacristid. They can be distinguished from the species of *Dorcopsis*, *Dorcopsulus* and *Dendrolagus* by possessing a broad, well-formed protolophid on M_1 , having a P^2 with a prominent posterolingual cusp and in possessing higher-crowned molars with better-developed links. They can be distinguished from *Hadronomas puckeridgei* by possessing higher-crowned molars with better-developed links and in having less strongly ridged and less bulbous premolars. They differ from species of *Macropus* and *Onychogalea* by lacking an arched alveolar margin to the lower molar row and in having much more elongate premolars which are retained throughout life. They can be distinguished from the species of *Dorcopsoides*, *Prionotemnus palankarinnicus* and the species of *Protemnodon* (except some *P. roechus*) in lacking a posterior cingulum on the lower molars. They differ from *P. roechus* by possessing higher-crowned, more elongate molars, in being smaller in size and in lacking a specialised, spatulate-like I_1 . They differ from *Setonix brachyurus* in possessing higher-crowned molars, having a non-fenestrate palate and in having a weaker lingual cingulum on P^3 . They differ from the species of *Thylogale*, *Petrogale*, *Lagorchestes* and *Macropus* wallabies in having a non-fenestrate palate and in being larger in size. The diastema of the dentary is relatively longer and the protolophid of M_1 wider than in the species of *Lagorchestes*. They differ from all *Macropus* wallabies in possessing lower-crowned molars with less convex hypolophid rear faces and (except *M. agilis*) in possessing proportionately much longer premolars. They can be distinguished from the species of *Wallabia* by possessing weaker pre- and post-metacristae on the upper molars and by possessing a non-fenestrate palate.

Etymology. *Kurrabi* is a New South Wales Aboriginal word for gully (McCarthy 1971), a reference to the postulated depositional environment of the Bow local fauna.

Discussion. The relationships of the species of *Kurrabi* are at present unclear. The closest affinities seem to lie with a group of macropodines including the species of *Protemnodon*, *Wallabia* and some *Macropus*. All of these forms possess moderately hypsodont molars and elongate, permanent premolars. A thorough cladistic analysis of the Macropodinae (in progress) should enable a better understanding of the nearest relatives of the otherwise distinctive species of *Kurrabi*.

Species of *Kurrabi* are restricted in distribution, being known only from the Bow and Hamilton local faunas (Flannery *et al.* in prep.). However, where they

occur, they are abundant. For example, *Kurrabi mahoneyi* is the second and *K. merriwaensis* the third most abundant macropodoids in the Bow local fauna.

Kurrabi mahoneyi n. sp.
(Figures 1H-K and 2; Table 2)

Holotype. AM F64016, partial left dentary containing I_1 , P_{2-3} and M_{1-3} , which is broken away posterior to M_3 .

Referred specimens. AM F64018, right dentary containing I_1 , P_2 , M_{1-2} (judging from wear patterns, stage of eruption of molars and preservation, this specimen may be from the same individual as the holotype). AM F60114, left dentary fragment containing P^2 , P^3 , M^{1-3} . AM F64019, right maxillary fragment containing M_{2-5} . AM F64022, right dentary fragment containing M_{2-5} . AM F64024, left dentary fragment containing P_3 , M_2 . AM F59572, left dentary fragment containing partial P_3 , M_1 , complete M_{2-4} . AM F59561, right dentary fragment containing P_3 . AM F59577, left P_3 fragment. AM F64029, left M_1 . AM F64028 and AM F64031, left P_3 fragments. AM F59603, right maxillary fragment containing P^3 , M^{2-5} . AM F64023, left maxillary fragment containing P^3 , M^{2-5} . AM F64020, left maxillary fragment containing P^2 , P^3 , M^{1-3} . AM F64019, right maxillary fragment containing P^3 fragment, M^{1-2} . AM F59562 and AM F64030, left P^3 's. AM F64026, right P_3 . AM F64027, right P^3 fragment. AM F64025, left P^3 fragment.

Diagnostic features. *Kurrabi mahoneyi* can be distinguished from *K. merriwaensis* n. sp. in possessing more elongate premolars, less well-developed postparacristae and premetacristae on the anterior molars and a better-developed premetacristid on M^1 which reaches the anterior part of the anterior cingulum. Also the P^3 of *K. mahoneyi* possesses three small cusps between the anterior and posterior cusps, while that of *K. merriwaensis* usually possesses only two.

Type locality and age. All specimens were recovered from a road cutting on the Merriwa-Cassilis Road, 500 m west of Bow Creek, 12 km west of Merriwa, New South Wales (Grid reference 323033 on 1:250,000 geological sheet for Singleton, No 51-56-1, New South Wales Department of Mines, Sydney). The Bow local fauna is generally believed to be early Pliocene in age (Skilbeck 1980).

Etymology. This species is named in honour of J. A. Mahoney who was instrumental in the initial investigation of the Bow fossil locality and who subsequently collected much of the material described here.

Description. Maxilla. The palate appears to have been non-fenestrate. The prominent masseteric process is present composed solely of the maxillary. The position of the infraorbital foramen cannot be determined.

The P^2 is elongate and possesses a main crest composed of an anterior and posterior cusp with a single strong ridge between. A distinct posterobuccal cusp, which is lower than the main crest, joins it by two ridges, one running directly to the posterior cusp and the other running posterobuccally to join it more

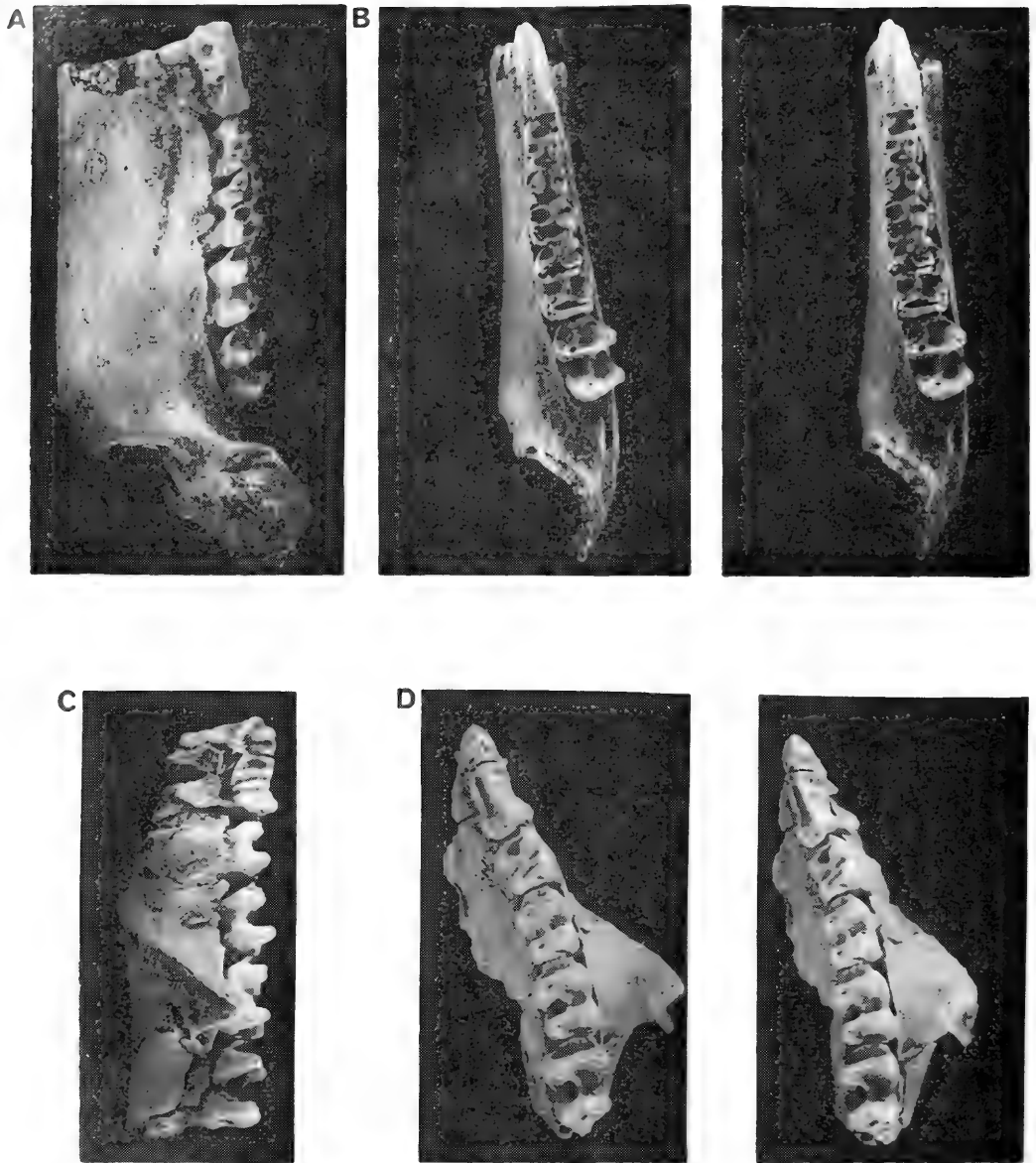


Fig. 2. A, lingual view of AM F60114, adult left dentary of *Kurrabi mahoneyi*, X1. B, stereopair of occlusal view of same specimen, X1. C, lingual view of AM F59603, adult right maxillary fragment of *K. mahoneyi* containing P^3 , M^{2-5} , X1. D, stereopair of same specimen, X1.

PLIOCENE KANGAROOS FROM THE BOW LOCAL FAUNA, N.S.W.

TABLE 2. Dental measurements of *Kurrabi mahoneyi* n. sp. from the Bow local fauna. Measurements are in mm. X = mean, R = range, L = length, AW = anterior width, PW = posterior width, STD = standard deviation, N = number.

		X	R	STD	N
P ²	L	10.3			1
	AW	4.2			1
	PW	4.5			1
P ³	L	15.5	15.1-16.2	.52	6
	AW	4.7	4.2- 5.2	.29	6
	PW	6.5	6.0- 6.9	.37	6
M ¹	L	8.5	8.5		2
	AW	6.1	6.0- 6.2		2
	PW	6.4	6.3- 6.4		2
M ²	L	9.1	8.4-10.0		4
	AW	7.2	6.9- 7.4		4
	PW	7.1	6.8- 7.6		4
M ³	L	10.0	9.4-10.5		3
	AW	7.9	7.7- 8.0		2
	PW	7.4	7.4		2
M ⁴	L	10.8	10.6-10.9		2
	AW	8.5	8.4- 8.6		2
	PW	7.9	7.8- 7.9		2
M ⁵	L	11.2	11.2		2
	AW	8.5	8.4- 8.5		2
	PW	7.2	7.0- 7.3		2
P ₂	L	8.4	8.3- 8.4		2
	AW	3.4	3.3- 3.5		2
	PW	3.8	3.6- 4.0		2
P ₃	L	12.8	11.9-13.2	.51	5
	AW	4.0	3.8- 4.3	.21	5
	PW	4.0	3.9- 4.2	.11	7
M ₁	L	8.2	8.1- 8.4		3
	AW	4.2	4.0- 4.3		3
	PW	5.0	4.8- 5.2		4
M ₂	L	9.3	8.7-10.3		3
	AW	5.7	5.5- 6.0		3
	PW	5.9	5.5- 6.2		3
M ₃	L	10.0	9.1-11.0	.72	5
	AW	6.6	6.2- 7.0		2
	PW	6.5	6.5		2
M ₄	L	10.5	10.1-10.9		3
	AW	7.6	7.4- 7.8		2
	PW	7.7	7.7		2
M ₅	L	12.2	11.9-12.5		3
	AW	7.9	7.7- 8.1		3
	PW	7.1	6.9- 7.3		3

posteriorly. These ridgelets enclose a posterior fossette. A well-developed lingual cingulum is present on the posterior two-thirds of the tooth with low tubercles continuing further anteriorly than this.

The P³ is a large tooth relative to molar size. The main crest is composed of an anterior and posterior cusp with three distinct cuspsules and associated

ridgelets between. The distinct posterolingual cusp is lower than the main crest and is joined to it by two ridges, one running directly to the main crest and the other (lower) ridge running around the posterior border of the tooth. These ridges enclose a posterior fossette. The continuous, low lingual cingulum extends two-thirds to three-quarters of the length of the tooth from the posterior margin with one or two low tubercles continuing further anteriorly. These end opposite the anterior cusp. The P^3 is slightly constricted one-third of the way from the posterior end of the tooth.

Upper molars. The anterior cingulum of M^1 is connected to the paracone buccally by a prominent preparacrista. Lingually the anterior cingulum fuses with the base of the protoloph anterior to the apex of the protocone. A slight forelink may be present (as in AM F64019). The protoloph is weakly-formed. The protocone and, to a greater extent, the paracone form distinct prominences on the protoloph. The postparacrista is strongly-developed and a weaker premeracrista is present. The midlink originates at the apex of the protocone and extends across the narrow interloph valley to terminate against the anterior face of the hypoloph between the hypocone and the metacone. The metacone and, to a lesser extent, the hypocone form distinct prominences on the hypoloph. The posthypocrista is well-developed and unites with a much less well-developed, near-vertical postmetacrista. A slight postlink is present. The M^2 differs from M^1 in the following ways: it is larger; the pre- and postparacrista are greatly reduced in strength; the premetacrista is absent; the anterior cingulum appears to be more restricted lingually; the protoloph is better-developed and the cones are of a more equal height; a postlink is absent; the midlink has a distinct fissure near its posterior end suggesting that the posterior moiety is a contribution from the hypoloph and the anterior portion is from the postprotocrista (this area is obscured by wear on M^1). The M^3 differs from M^2 in being larger and in having the pre- and postparacristae and the posthypocrista further reduced. M^4 is similar to M^3 but is larger. The M^5 differs from M^4 in that the hypoloph is narrower than the protoloph.

Dentary. A groove runs from below the anterior end of M_2 to P_2 in the holotype. The mandibular symphysis is weakly-ankylosed. The mental foramen is situated approximately 6 mm anterior of the anterior root of P_2 on the holotype. The ventral margin of the dentary is almost straight.

The I_1 is enamelled buccally with a distinct and well-developed flange of enamel ventrally and dorsally. A thin veneer of enamel is present ventrolingually. The tooth is high dorsoventrally and narrow buccolingually.

The P_2 consists of a simple, straight blade with an anterior and posterior cuspid. It has two smaller cuspsules and associated ridgelets between them. There is a very slight posterolingual flexion of the crest.

The P_3 is an elongate tooth consisting of a main crest of even height, possessing a posterior and anterior cuspid with three smaller cuspsules and associated

ridges in between. Distinct buccal and lingual ridges run to the crown base from the anterior cuspid. There is a slight posterolingual flexion of the crest. The tooth is slightly constricted about one quarter of the way anteriorly from its posterior end.

Lower molars. The anterior cingulum of M_1 is narrow and high. A nearly straight paracristid is present near the buccal edge of the anterior cingulum. Further buccal to the paracristid is a slight extension of the anterior cingulum. Lingually, the anterior cingulum is bounded by a strong premetacristid. The protolophid, which is narrower than the hypolophid, is weakly-formed. The metaconid and, to a lesser extent, the protoconid form distinct prominences. The cristid obliqua runs from the hypoconid to the posterior face of the protoconid. A slight postmetacristid and even weaker preentocristid tend to block the lingual interlophid valley. The entoconid and, to a lesser extent, hypoconid form distinct prominences on the hypolophid. The rear face of the hypolophid is vertically oriented and unornamented. The M_2 differs from M_1 in the following ways: it is larger; it lacks a premetacristid; the paracristid is shifted more lingually and is concave buccally rather than being straight; the cristid obliqua is also more concave buccally and more centrally placed than on M_1 ; the conids are of a more equal height; and the postmetacristid is absent. The M_3 differs from M_2 mainly in being larger and in possessing a slight pit on the rear face of the hypolophid (on the holotype only). The M_4 is similar to M_3 except that it is larger. The M_5 is larger than M_4 and has a slightly narrower hypolophid than protolophid, but is otherwise similar.

Discussion. *Kurrabi maboneyi* and *K. merriwaensis* are very similar in dental morphology, differing mainly in premolar size and details of anterior molar morphology. The difference in premolar size between these forms may indicate a dietary difference, *K. maboneyi* with its larger premolars possibly being capable of severing larger twigs and leaves than *K. merriwaensis*.

Kurrabi merriwaensis n. sp.
(Figures 3-4; Table 3)

Holotype. AM F64014, left dentary fragment containing P_2 , P_3 , M_{1-4} . The dentary is broken away anterior to the P_2 and posterior to M_4 .

Referred specimens. AM F59570, left fragmentary dentary containing P_3 , M_{2-5} . AM F59531, right dentary fragment containing P_3 , M_{2-5} . AM F64015, left dentary fragment containing P_3 , M_1 . AM F64032, left P_3 . AM F59590, right maxillary fragment containing P^3 , M^{2-5} . AM F64013, left maxillary fragment containing P^2 , P^3 , M^{1-3} . AM 640115, right maxillary fragment containing a fragmentary P^3 , M^{2-4} .

Diagnostic features. *Kurrabi merriwaensis* can be distinguished from *K. maboneyi* in that the premolars are shorter absolutely and relative to molar size, the pre- and postparacrista are better-developed on anterior upper molars and the premetacristid on M_1 does not contact the anterior edge of the anterior cingulum.

TABLE 3. Dental measurements of *Kurrabi merriwaensis* n. sp. from the Bow local fauna. L = length, AW = anterior width, PW = posterior width.

		L	AW	PW
F 64013	P ²	9.3	4.4	5.5
	P ³	12.8	3.3	6.4
	M ¹	8.9	6.2	6.8
	M ²	9.3	7.6	7.7
	M ³	10.8	7.8	
F 59590	P ³	12.2	4.1	5.9
	M ²	9.4		
	M ³	10.3		8.5
	M ⁴	11.4		7.4
	M ⁵	12.1	9.0	
F 60115	M ¹	8.3	6.6	6.6
	M ²	8.8	7.4	7.0
	M ³	11.0	8.2	7.8
F 64032	P ³	11.2	3.2	3.6
F 64015	P ³	11.0	3.2	3.2
	M ₁	8.0	4.7	5.1
F 64014				
(Holotype)	P ₂	7.8	3.0	3.0
	P ₃	11.1	2.9	3.7
	M ₁	8.2	4.6	5.3
	M ₂	10.4	6.1	6.5
F 59531	P ₃	10.0	3.0	3.2
	M ₂	8.1	5.2	5.7
	M ₃	9.0	6.4	6.6
	M ₄	10.9	7.6	7.6
	M ₅	11.9	7.5	6.7
F 59570	P ₃	10.0	3.3	3.3
	M ₂	8.3		
	M ₃	9.9	6.8	6.7
	M ₄	10.2	7.5	7.6
	M ₅	11.8	7.7	7.0

Type locality and age. As for *Kurrabi mahoneyi*.

Etymology. This species is named in honour of the Merriwa Shire Council employees who have been very helpful to the various expeditions from the University of New South Wales and the Australian Museum. In particular, the help and support of Mr Greg Coulson and Mr I. Tiley given to the staff and students of the U.N.S.W. during the previous five years is most gratefully acknowledged.

Description. The Maxilla. Maxillary fragments reveal that *Kurrabi merriwaensis* most probably had a non-fenestrate palate (the median edge of the palate is unknown). The infraorbital foramen opens above the junction of P³ and M². The masseteric process is prominent and composed solely of the maxillary.

The P². The P² is elongate with a straight main crest and a posterolingual cusp. The main blade consists of an anterior and posterior cusp with a strong

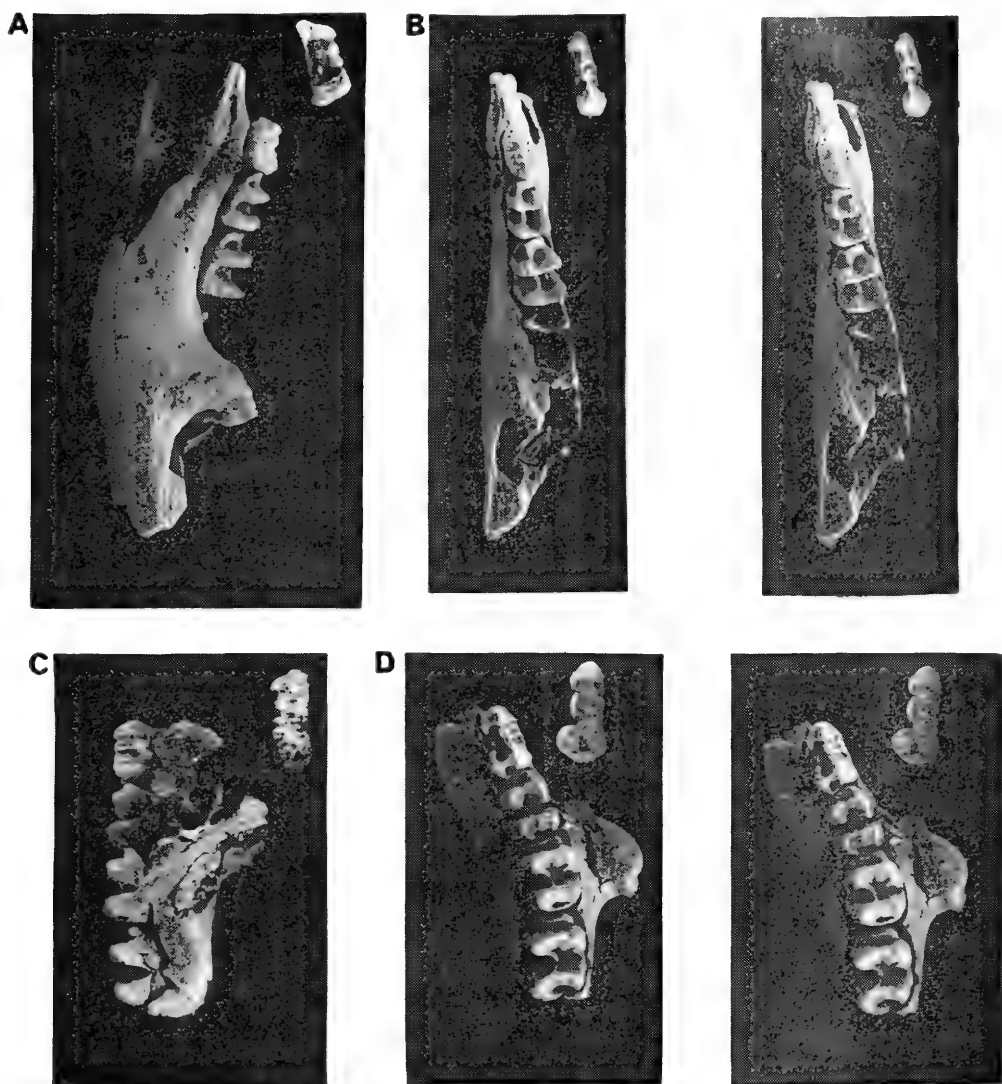


Fig. 3. A, lingual view of holotype of *Kurrabi merriwaensis* (AM F64014), containing P₂, P₃ (removed from crypt), M₁₋₂, M₃₋₄ in crypt, X1. B, stereopair of occlusal view of same specimen, X1. C, lingual view of AM F64013, juvenile left maxillary fragment of *K. merriwaensis* containing P₂, P₃ (removed from crypt), M₁₋₃, X1. D, stereopair of occlusal view of the same specimen, X1.

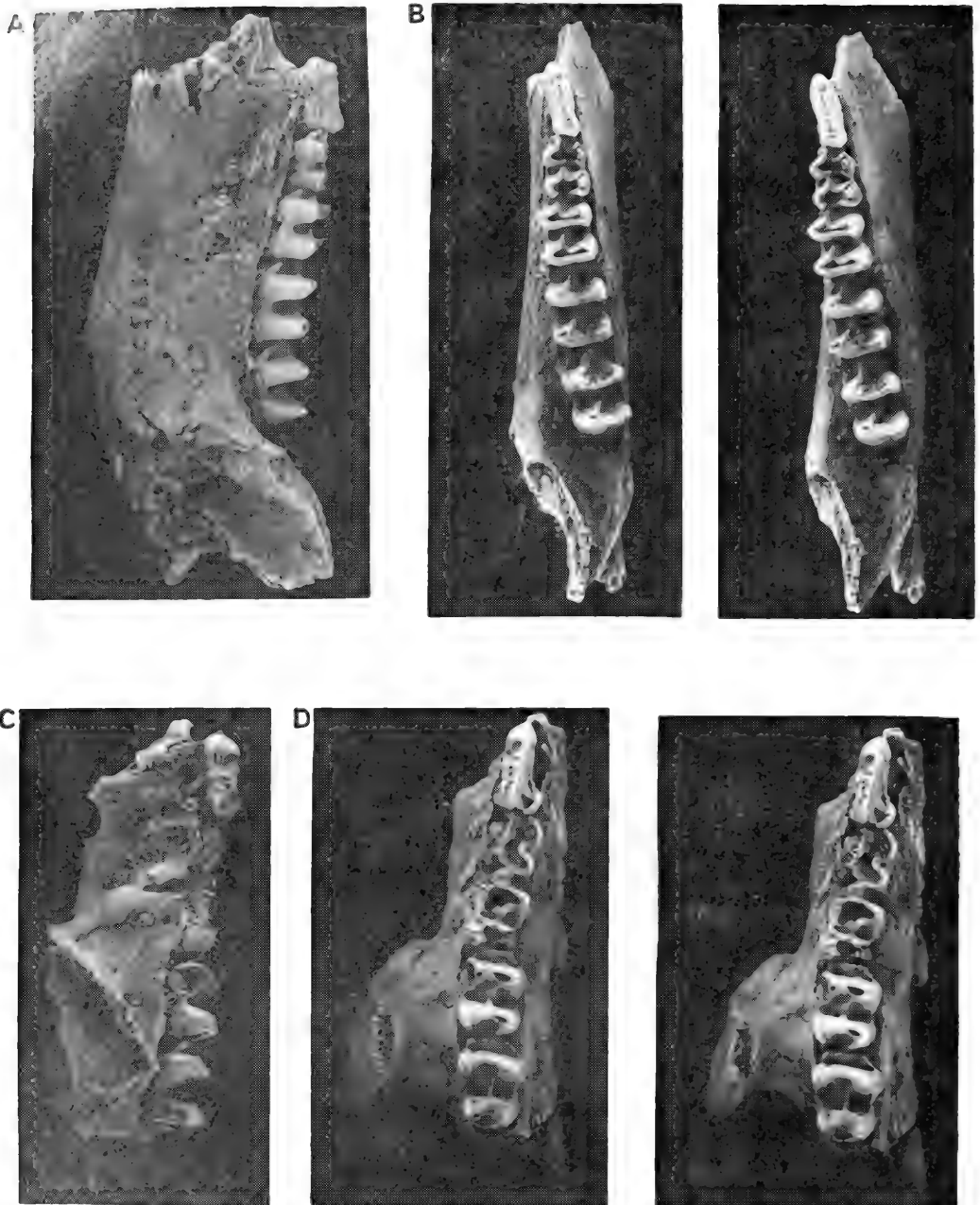


Fig. 4. A, lingual view of AM F59570, adult dentary fragment containing P₃, M₂₋₅ of *Kurrabi merriwaensis*, X1. B, stereopair of occlusal view of the same specimen, X1. C, lingual view of AM F59590, adult maxillary fragment containing P³, M^{3.5} of *K. merriwaensis*, X1. D, stereopair of occlusal view of the same specimen, X1.

ridge and associated cuspule between. A moderately well-developed lingual cingulum extends from the posterolingual cusp to opposite the anterior cusp. The lingual cingulum is formed of small tubercles and is markedly constricted two-thirds of the way from its posterior end. The posterolingual cusp is approximately one-half the height of the main crest and is attached to it by a well-developed, straight anterior crest and a weaker posterior crest, which first runs posteriorly, then turns sharply buccally. A large posterior fossette is enclosed by these ridges.

The P^3 . The P^3 consists of a main blade and a posterolingual cusp. The blade consists of a prominent anterior and posterior cusp with three smaller cuspules and associated ridgelets in between. The posterolingual cusp is two-thirds the height of the main blade. A small cuspule is present posterolingual to the main blade and posterobuccal to the posterolingual cusp. The low, rounded lingual cingulum ends anteriorly opposite the anterior cusp.

Upper molars. The protoloph of M^1 is weakly-developed, possessing a paracone and metacone that form distinct prominences. The paracone is higher than the protocone and possesses a distinct preparacrista that joins the anterior cingulum. A small forelink is present anterior to the protocone. The anterior cingulum extends to near the lingual edge of the tooth. A very well-developed postparacrista joins a well-developed premetacrista to block the buccal end of the narrow interloph valley. However, a small portion of the valley extends buccal to this. The midlink originates from the protocone and terminates in the centre of the anterior face of the hypoloph. The posthypocrista is very well-developed and joins a near vertical postmetacrista. A small postlink is present on the rear face of the hypoloph, slightly closer to the metacone than the hypocone. The M^2 differs from M^1 in the following ways: it is larger; the preparacrista is more weakly-developed; the protoloph is more strongly-developed; the postparacrista and premetacrista are less well-developed and shifted slightly more medially; the anterior cingulum is more restricted lingually; the forelink is absent; the midlink has a fissure near its posterior end (this area is obscured by wear on M^1) suggesting that its posterior portion is a contribution from the hypoloph; and the postlink is much more weakly-developed. The M^3 differs from M^2 in the following ways: it is larger and the preparacrista is less well-developed; the postparacrista and premetacrista are also more weakly-developed; and the postlink is absent. The M^4 is larger than M^3 . It lacks a preparacrista and the postparacrista and premetacrista are further reduced or absent relative to M^3 . The M_5 is similar to M_4 except that the hypoloph is narrower than the protoloph.

Dentary. The dentary is unknown anterior to P_3 . The position of the mental foramen and the morphology of the ascending ramus are also unknown. A slight buccinator groove is present extending from a position below the posterior end of M_2 to just anterior to P_3 on the buccal side of the dentary. The ventral border of the dentary of the holotype is almost straight but it turns dorsally posterior to the erupted molar row.

The P_2 forms an elongate blade which is slightly convex buccally with a distinct posterolingual flexion. There is a distinct anterior and posterior cuspid with two smaller cuspules and associated ridges between.

The P_3 is larger than P_2 but is of an essentially similar morphology. It differs in being straighter and in the posterior cuspid being slightly more bulbous. As with P_2 , two small cuspules are present between the anterior and posterior cusps. In AM F64032, a small third cuspule is developed posterior to the other two.

Lower molars. The M_1 possesses a narrow anterior cingulum, slightly more so in AM F64015 than AM F59570 or AM F59531. The paracristid is well-developed and runs from the metaconid to near the buccal side of the anterior cingulum. The preprotocristid is strongly developed but stops well short of the anterior end of the anterior cingulum. The metaconid and, to a lesser extent, the protoconid form distinct prominences on the protolophid which is narrower than the hypolophid. The cristid obliqua is well-developed, running across the deep interlophid valley. It originates from the hypoconid and joins the posterior portion of the metaconid. The entoconid and, to a lesser extent, the hypoconid form distinct apices on the hypolophid. There is a very slightly-developed prehypocristid. M_2 differs from M_1 in the following ways: it is markedly larger; the paracristid is more strongly-concave buccally; the preprotocristid is absent; the protolophid is the same width as the hypolophid; the conids do not form such prominent apices on the lophid margins; the cristid obliqua joins the posterior face of the protolophid further lingually and is more concave buccally; the prehypocristid is reduced in strength but retained as a small fold of enamel in the lingual side of the interlophid valley; and a very slight depression is present on the posterior face of the hypolophid. The M_3 differs from M_2 in the following ways: it is larger; the prehypocristid is slightly less distinct; the conids at the loph corners are less prominent. The M_4 is larger than M_3 but is otherwise similar. The M_5 is more elongate and narrow than M_4 and the hypolophid is reduced in size. The width of the anterior cingulum varies considerably on the known specimens of *K. merriwaensis*. On AM F59531, the anterior cingula are broader on the posterior molars than on other specimens and possess a distinct anteroposteriorly-oriented ridge on their buccal margins.

Discussion. *Kurrabi merriwaensis* is most similar to an unnamed species of *Kurrabi* from the Hamilton local fauna (Flannery *et al.* in prep.). These two species differ mainly in the degree of hypsodonty of the molars. However, the Hamilton form has much lower-crowned molars with a more weakly-developed cristid obliqua and paracristid. This may indicate that it is a more primitive species than *K. merriwaensis*, or that it occupied a different habitat, or both. The Hamilton local fauna suggests a rainforest habitat (Turnbull and Lundelius 1970, Flannery *et al.* in prep.) while the Bow local fauna suggests a savannah woodland or open forest.

Protemnodon Owen, 1874

Protemnodon chinchillaensis Bartholomai, 1973.

(Figure 5A,B)

Material. AM F64034, left dentary containing P_3 , M_{2-5} . AM F59549, left dentary fragment containing M_2 . AM F59537, left dentary fragment containing M_3 . AM F64036, right lower molar. AM F64041, AM F64040 and AM F64037, lower molar fragments. AM F64039 and AM F64044, lower premolar fragments. AM F59533, left maxillary fragment containing P^3 , M^{2-3} . AM F59530, left maxillary fragment containing M^{2-5} . AM F59606, left maxillary fragment containing M^{3-4} . AM F64035, right maxillary fragment containing fragmentary M^{3-5} . AM F64042, right M^3 . AM F64038, upper molar fragment. AM F64043 and AM F64045, upper premolar fragments. AM F60118 and AM F59610, I^1 's of *Protemnodon* sp. cf. *P. chinchillaensis*.

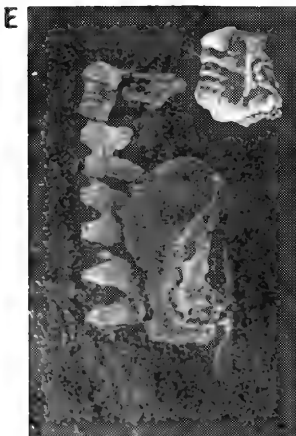
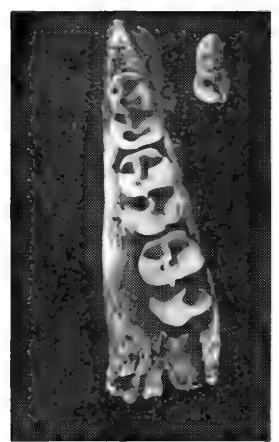
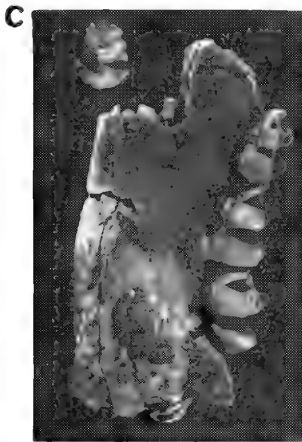
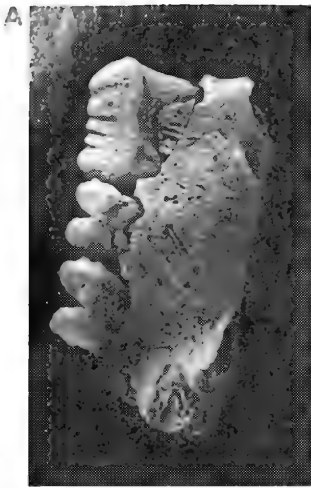
Diagnostic features. This material is most similar in size and morphology to *Protemnodon chinchillaensis*. It can be distinguished from *P. buloloensis* by its larger size and more bulbous P_3 . It lacks the postlink present on the anterior upper molars of *P. otibandus*. It has lower-crowned molars and is smaller than *P. roechus*, *P. brebus*, *P. devisi* and *P. anak*. It can be distinguished from *P. devisi* and *P. snewini* by possessing proportionately longer premolars relative to molar length (see Fig. 5A, B, Table 1).

Discussion. The I^1 's tentatively referred here to *P. chinchillaensis* are robust and very similar in shape to the I^1 of *P. anak*. They are too large to belong to either *K. mahoneyi* or *K. merriwaensis*. Both specimens possess a heavily worn crown and a thick root which is oval in cross-section. Enamel is restricted to the anterior surface of the tooth. The wear facet ascends the tooth in a gentle postero-dorsal arc. This arcuate-shaped wear facet appears to be the result of the anterior enamel face being more resistant to abrasion than the dentine.

In the course of comparing the Bow material of *P. chinchillaensis* to that of other species of *Protemnodon*, the specimen tentatively referred to *P. otibandus* by Plane (1972) from the early Pliocene marine Jemmy's Point Formation, Victoria, was re-examined. We found that it lacks the postlink that is present on the anterior upper molars of *P. otibandus*, but absent in *P. chinchillaensis*. This is the only feature of the Jemmy's Point specimen that allows for referral to *P. chinchillaensis* rather than *P. otibandus*. For this reason, it is here referred to *P. chinchillaensis* Bartholomai, 1973. The Jemmy's Point specimen represents the third locality record of *P. chinchillaensis* (the others being at Bow, N.S.W. and Chinchilla, Qd) and a considerable geographic range extension.

cf. *Protemnodon* sp.

Material. A single tooth fragment, AM F64006, may represent a second species of *Protemnodon* in the Bow local fauna. It is the central portion of the main crest of a left P^3 , lacking the anterior and posterior ends and the lingual cingulum.



PLIOCENE KANGAROOS FROM THE BOW LOCAL FAUNA, N.S.W.

Description. This specimen is much larger than an equivalent fragment from *P. chinchillaensis*. Buccally, three coarse ridglets, separated by "U"-shaped depressions, are restricted to near the apex of the cutting crest. Lingually, a further three coarse ridglets are present but extend further towards the tooth base. The lingual side of the fragment slopes less steeply to the base than does the buccal side.

Discussion. Although this fragment appears to represent a distinctive species, it is too incomplete to permit confident taxonomic appraisal.

Macropus Shaw, 1970
Macropus dryas (DeVis, 1895)
(Figure 5E,F)

Material. AM F59546, left dentary containing a fragment of the P_3 , M_{2-3} and a talonid of M_4 . AM F59535, left maxillary fragment containing P^2 , P^3 , M^{1-3} . AM F64064, left M^3 . AM F64065, right M^2 .

Diagnostic features. This material has been assigned to *Macropus dryas* for the following reasons: the premolars are elongate and the lingual cingulum of the P^3 is reduced to a series of low tubercles; the molars are high-crowned; the upper molars invariably possess well-developed forelinks; the rear face of the hypophid of the lower molars is convex with no ornamentation; the anterior cingulum is high; and the paracristid and cristid obliqua are well-developed (see Fig. 5E,F). In possessing a combination of these characteristics, the Bow material closely resembles *M. dryas* and is distinct from other macropodoid species.

Discussion. The genus *Macropus* is currently under revision by Dawson and Flannery (in prep.). The subgeneric affinities of *M. dryas* are at present uncertain.

The Bow specimens of *M. dryas* are slightly smaller than the *M. dryas* material from Allingham reported by Bartholomai (1978), both samples of which contain smaller individuals again than the *M. dryas* sample from Chinchilla (Bartholomai 1975). AM F59546, the dentary, is rather poorly-preserved and the molars of this specimen rise into occlusion steeply, a characteristic not well-developed in any figured specimens of *M. dryas* reported by Bartholomai (1975, 1978). Although tenuous, the smaller size of the Allingham and Bow material may be further evidence of a closer temporal relationship between the Bluff Downs and Bow local faunas than between the Bow and Chinchilla local faunas (see Table 1).

Fig. 5. A, lingual view of AM F59533, left maxillary fragment containing P^3 , M^{2-3} of *Protemnodon chinchillaensis*, X1. B, stereopair of occlusal view of the same specimen, X1. C, lingual view of AM F64033, left dentary fragment containing P_3 (removed from crypt), M_{1-3} of *Macropus (Osphranter) pavana*, X1. D, stereopair of occlusal view of the same specimen, X1. E, lingual view of AM F59535, left maxillary fragment containing P^2 , P^3 (removed from crypt), M^{1-3} of *Macropus dryas*, X1. F, stereopair of occlusal view of the same specimen, X1.

Macropus (Osphranter) Gould, 1842
Macropus (Osphranter) pavana Bartholomai, 1978
 (Figure 5C,D)

Material. AM F59534, left dentary fragment containing P₃, M₃. AM F59573, left dentary fragment containing P₃, M₁, M₃. AM F64033, left dentary fragment containing P₃, M₁₋₃. AM F59548, left dentary fragment containing M₂₋₄. AM F59585, right dentary fragment containing M₃₋₅. AM F64055, left dentary fragment containing M₅. AM F59578, AM F64052 and AM F64046, lower molar fragments. AM F59536, right maxillary fragment containing M₁₋₅. AM F64047, right maxillary fragment containing M₃₋₄. AM F59532, left maxillary fragment containing M³. AM F64050, AM F64054, AM F64051, AM F64053, AM 64047 and AM F64048, isolated upper molars and tooth fragments.

Diagnostic features. In size and morphology these specimens most closely resemble *Macropus (Osphranter) pavana* from the Bluff Downs local fauna, north-eastern Queensland. Unfortunately, comparisons are hampered by the rarity of *M. (O.) pavana* remains at Bluff Downs. The Bow material differs from *M. (O.) woodsi* (apparently a closely related form) in the following ways: it lacks the accessory cuspules on the median side of the interloph valleys; it has less well-developed forelinks on the upper molars; it has a more trenchant, blade-like P₃ which is not divided into discrete large cuspules.

Discussion. Some differences exist between the Bow and Bluff Downs samples of *Macropus (Osphranter) pavana*. On the three upper molars assigned to *M. (O.) pavana* from Allingham, a well-developed forelink is present. Such a structure can be distinguished on only three of the nine molars assigned to *M. (O.) pavana* from Bow. However, in several of the Bow specimens, a forelink (if present) may have been removed by wear. This difference is not considered significant at the species level because forelink development is variable in the living species of *M. (Osphranter)* (Flannery 1981) and because the sample size for *M. (O.) pavana* is extremely small. A single P₃ of *M. (O.) pavana* is known from Allingham. This specimen has a single small cuspule between the larger anterior and posterior cuspids. All three specimens of P₃ of *M. (O.) pavana* from Bow have two small cuspules in this position. The number of cuspules between the anterior and posterior cuspids on P₃ of *M. giganteus* and *M. fuliginosus* have been shown to vary between zero and one (Bartholomai 1971, Flannery 1981), so this difference also is not considered sufficient to recognise a separate species for the Bow material. The P₃ of F64033 from Bow differs from the other specimens in possessing a tall posterobuccal cuspid which is separated from the main crest by a deep fissure (see Fig. 5C,D). This is considered to represent an abnormal specimen because it differs so radically from the P₃ of other specimens.

Macropodinae indet. Type 1

Material. A left dentary fragment AM F64001, containing a partial M₃₋₄, represents a small macropodine in the Bow local fauna.

Description. The dentary is markedly narrow buccolingually; below the anterior end of M_3 it is narrower than the base of the crown of that tooth. A groove, originating below the anterior end of M_4 , runs anteriorly under M_3 on both the buccal and lingual sides of the dentary. No detailed morphology can be seen on M_3 because it is too worn and broken. The M_4 , however, lacks only the metaconid. Both lophids are breached by wear. The anterior cingulum is low and relatively broad. The paracristid, which originates near the protoconid (the exact relationship being obscured by wear) and ends in the anteromedial portion of the anterior cingulum, is strongly-developed. The cristid obliqua runs from near the hypoconid (the exact relationship being obscured by wear) to the medial part of the rear face of the hypolophid. The lophids are wider at the apex than the base. No posterior cingulum can be seen. However, if it was a small structure it could have been obliterated by the large interdental wear facet developed on the rear face of the hypolophid.

Discussion. Although it is clear that this specimen belongs to a species of macropodine approximately the size of *Macropus rufogriseus*, it is too fragmentary to permit other than subfamilial determination.

Macropodinae indet. Type 2

Material. A tiny protoloph (AM F64008), possibly of an M^2 , and two tiny hypolophids (AM 64009 and AM F64010) represent a macropodine of approximately the size of *Dorcopsulus vanheurni*.

Description. The protoloph fragment is unworn and low-crowned. The apex of the protoloph is markedly narrower than its base. A small preparacrista joins buccal end of the anterior cingulum. The anterior cingulum becomes indistinct near the lingual loph margin. The protoloph apex is convex anteriorly. The post paracrista and postprotocrista are well-developed. They approximate and almost meet in the medial part of the base of the posterior side of the protoloph. The hypolophid fragments lack a posterior cingulum and possess a weakly-developed cristid obliqua that originates at the hypoconid. A rounded preentocristid is also present.

Discussion. These specimens represent the smallest macropodoid from Bow but, because of their fragmentary nature, they cannot be assigned to a genus.

DISCUSSION

An extremely diverse macropodoid assemblage, consisting of sixteen species (including hypsiprymnodontines, potoroinae, sthenurines and macropodines) is represented in the Bow local fauna. *Troposodon bowensis* Flannery and Archer, 1983 is the most abundant species, followed in order of abundance by *Kurrabi mahoneyi*, *K. merriwaensis*, *Macropus (Osphranter) pavana* and *Protemnodon chinchillaensis*. A species of *Propleopus*, a small species similar to *Dendrolagus*, a potoroine and a fragment not assignable to genus (but distinct from other taxa in the fauna), are the rarest elements, being represented by a single specimen

each. Most of the common forms possess hypsodont molars and elongate premolars. Living species with a similar dental morphology (e.g. *Macropus agilis*) inhabit woodland and savannah. The abundance of these forms, combined with the presence of a species of *Macropus* (*Osphranter*), all the living species of which inhabit rocky areas or dry regions, suggest that the Bow local fauna is derived from a woodland/savanna habitat.

Where related species exist at Bow and Hamilton, such as *Kurrabi merriwaensis* and the unnamed species of *Kurrabi* from the Hamilton local fauna (Flannery *et al.* in prep.), the Bow form has the more hypsodont molars. The Hamilton fauna is believed to represent a rainforest habitat (Turnbull and Lundelius 1970; Flannery *et al.* in prep.). A few of the rarer elements in the Bow fauna, such as the brachydont species referred to cf. *Dendrolagus*, may indicate a rainforest component. Given the rarity and fragmentary nature of the remains of brachydont kangaroos in the Bow local fauna and the fluvial depositional environment, these possible rainforest elements may have been transported some considerable distance before coming to rest at the Bow site.

Because the Bow local fauna cannot be dated radiometrically, faunal comparisons must be used to date the site. Similarities exist between the kangaroos of the Bow local fauna, the Hamilton local fauna (dated at 4.46 mybp), the Bluff Downs local fauna (dated at 4.45 mybp) and the Chinchilla local fauna (undated by radiometric techniques). Although no kangaroo species are shared between the Bow and Hamilton local faunas, several striking similarities can be seen at higher taxonomic levels. Morphologically similar specimens referred to cf. *Dendrolagus* found at both of these sites are not known from any other Pliocene localities. Also, the species of *Kurrabi* are at present unique to the Bow and Hamilton local faunas. In particular, *K. merriwaensis* and an unnamed species from Hamilton appear to be closely related.

Similarities between the kangaroos of the Bluff Downs and Bow local faunas are also marked. *Macropus dryas* is found in both sites. It is also found at Chinchilla but the Bluff Downs and Bow forms are of a similar small size (see Table 1 and Bartholomai 1975, 1978). *Macropus* (*O.*) *pavana* is at present known only from the Bluff Downs and Bow local faunas. *Macropus* (*O.*) *woodsii*, an apparently closely related form, occurs at Chinchilla. If the current view that Bluff Downs is older than Chinchilla is accepted (e.g., see Archer and Wade 1976), then *M.* (*O.*) *pavana* may well be ancestral to *M.* (*O.*) *woodsii*. Both the Bow and Bluff Downs local faunas share small, primitive species of *Troposodon* not found elsewhere (*T. bluffensis* and *T. bowensis*). Also, more widely ranging species such as *Troposodon minor*, which is also found at Chinchilla and Bluff Downs, may be present at Bow (Flannery and Archer 1983).

Similarities between the kangaroos of the Bow and Chinchilla local faunas are less marked than between those of the Bow and Bluff Downs or Hamilton local faunas. Only one species, *Protemnodon chinchillaensis*, is seen at Chinchilla

and Bow but not at Hamilton or Bluff Downs. However, *P. chinchillaensis* is also found in the early Pliocene Jemmy's Point Formation, Victoria (see *P. chinchillaensis* discussion) and thus may be more widespread than previously suspected.

Overall, the greatest similarities of the Bow kangaroos lie with those of the Hamilton and Bluff Downs local faunas. Thus, the Bow local fauna is considered to be probably early Pliocene in age. Differences between these macropodid assemblages may be the result of slight temporal, geographic and/or habitat differences.

CONCLUSIONS

Sixteen species of macropodoids, including hypsiprymnodontines, potoroines, thenurines and macropodines are found in the Bow local fauna of central eastern New South Wales, Australia.

The dental morphology of most species indicate a savanna and/or woodland habitat but a few poorly-preserved specimens may represent rainforest forms. These latter are few in number and represented by very fragmentary remains. Given the fluviatile nature of the deposit, they may have been transported some distance before being incorporated in the deposit.

The Bow fossil kangaroo assemblage most closely resembles those of the Hamilton and Bluff Downs local faunas and is thus interpreted to be early Pliocene in age.

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APPENDIX 1

Appendix 1 lists all macropodoid dental remains from Bow not mentioned in the text or other publications. All are Australian Museum fossil specimens. Molars, dentary or maxillary fragments belong to *Kurrabi mahoneyi* and/or *K. merriwaensis*.

PLIOCENE KANGAROOS FROM THE BOW LOCAL FAUNA, N.S.W.

AM F64050-2, AM F64056-63, AM F64064-73, AM F64075, AM F64077-81, AM F64083-7, AM F64089-90, AM F59587, AM F59568, AM F59549, AM F59538, AM F59586, AM F59571, AM F59579, AM F59565, AM F59574, AM F59550, AM F59582, AM F64162, AM F64233, AM F64296.

Isolated molars or fragments of other species which cannot be closely identified.

AM F64092-120, AM F59613, AM F59568, AM F59583, AM F60116, AM F64234-48.

Isolated premolars and fragments.

AM F64249-64295.

Isolated lower incisors.

AM F59553, AM F59541, AM F59559, AM F59589, AM F59533, AM F59552, AM F59591, AM F59543, AM F59580, AM 64021-49.

Isolated upper incisors or premaxilla fragments.

AM F59612, AM F59554, AM F64297-64323.

The Spring Creek Locality, Southwestern Victoria, a Late Surviving Megafaunal Assemblage

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ABSTRACT

The Spring Creek site contains a diverse, late surviving megafaunal assemblage, in association with plant material dated at $19,800 \pm 398$ ybp. Flora from the locality indicates a lack of trees and includes species from both water stress and water associated environments. The combination of water associated plant species now inhabiting high altitudes with some animals today found only in arid regions may have been caused by the colder and drier climatic conditions prevalent during the last glacial maximum in south-eastern Australia.

Analysis of age structure of herbivores in the fauna suggests that successful recruitment into the population had almost ceased. Drought conditions may have been responsible for the failure to breed and ultimately for the death of the adults.

INTRODUCTION

Recent studies have revealed much about the climate, flora and fauna of Australia during the Pleistocene (Bowler *et al.* 1976, Colhoun 1977; Gillespie *et al.* 1978, Hope *et al.* 1977, Wyroll 1979). The general climatic scenario for the Late Pleistocene emerging from these studies is that Australia experienced a progressively cooler and drier climate culminating, in southeastern Australia, at around 16,000-18,000ybp with the height of the last glacial maximum. The transition, however, was not constant. Milder phases were interspersed with more extreme ones.

While consensus seems to have been reached regarding a general climatic history for the Pleistocene, other events of this epoch are still hotly debated. Primary among these is the nature of megafaunal extinction. Even the timing of the extinction of the larger Australian marsupials is not agreed upon. Some workers doubt that the megafauna survived beyond 30,000ybp. However, an increasing number of sites containing large extinct marsupials are being dated at between 20 and 30,000ybp or younger (e.g., Flood 1973, Gillespie *et al.* 1978, Hope *et al.* 1977 and this study). Factors cited as the cause of megafaunal

extinction are many and varied (e.g., Merrilees 1968, Witter 1978, Martin 1967 and Main 1978). The arguments relevant to the Australian situation have recently been reviewed by Horton (1980). Two factors, humans and climatic change, are most commonly cited. Merrilees (1968) states a case for man as a cause while Main (1978) has put an interesting case for climate. It was in the hope of shedding light on the timing and causes of megafaunal extinction that the Spring Creek site was excavated.

Appendix 1 lists Museum of Victoria numbers for the Spring Creek fossils.

GEOLOGY, GEOLOGIC SETTING AND AGE

The Spring Creek locality is situated in the valley of Spring Creek, a permanent spring fed drainage that arises 2-3 kilometres southeast of Mt Rouse,

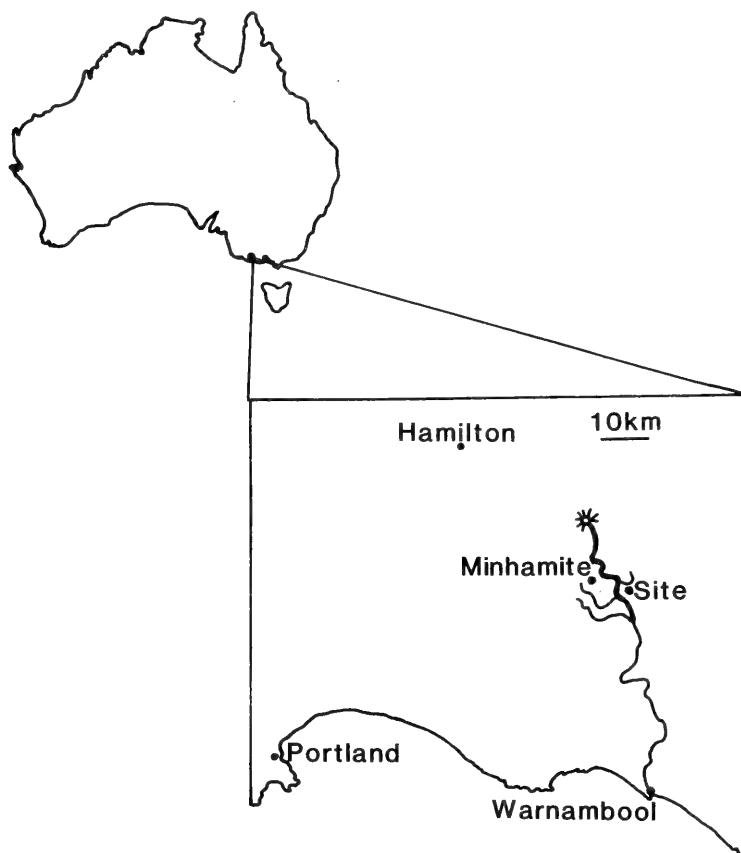


Fig. 1. Map showing location of the Spring Creek site: C = Caramut, H = Hamilton, M = Minhamite, P = Portland, Pe = Penshurst, W = Warnambool. The volcano just south of Penshurst is Mt. Rouse. The thick line = Spring Creek, the thin lines other waterways. X = the Spring Creek fossil locality.

SPRING CREEK MEGAFAUNAL ASSEMBLAGE



Fig. 2. Location of the Spring Creek site (photograph taken from the south).



Fig. 3. The Spring Creek fossil locality showing survey peg in south-western bank.

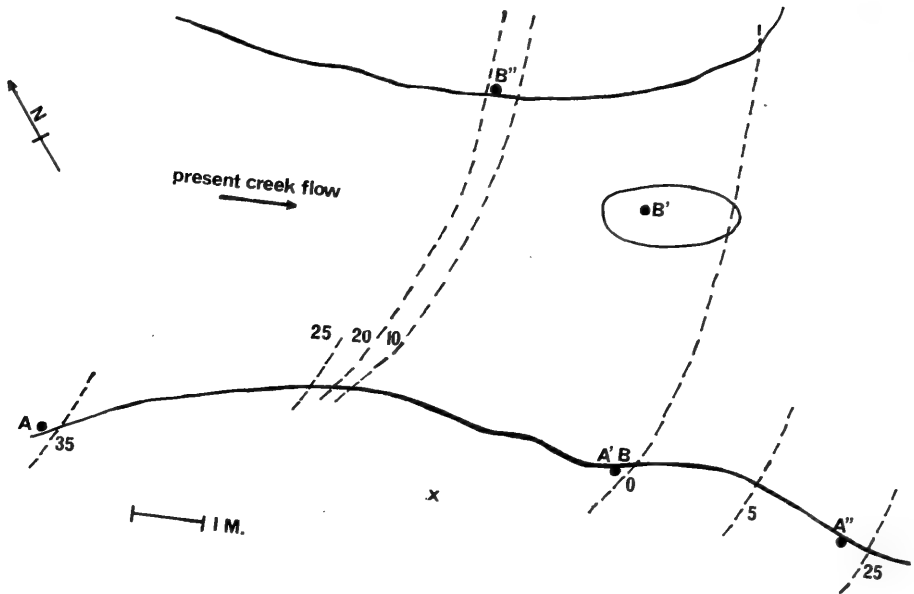


Fig. 4a. Plan of the fossil locality. Dashed lines with numbers = contours of the base of the Pleistocene sediments in cm relative to the lowest point of those sediments at point A'B.

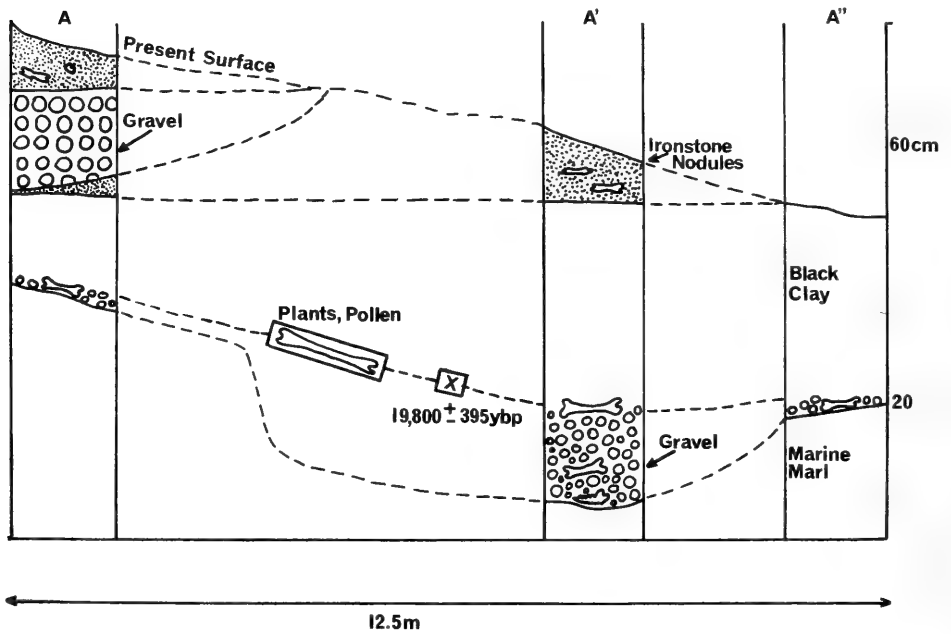


Fig. 4b. Section through site from A to A''.

SPRING CREEK MEGAFAUNAL ASSEMBLAGE

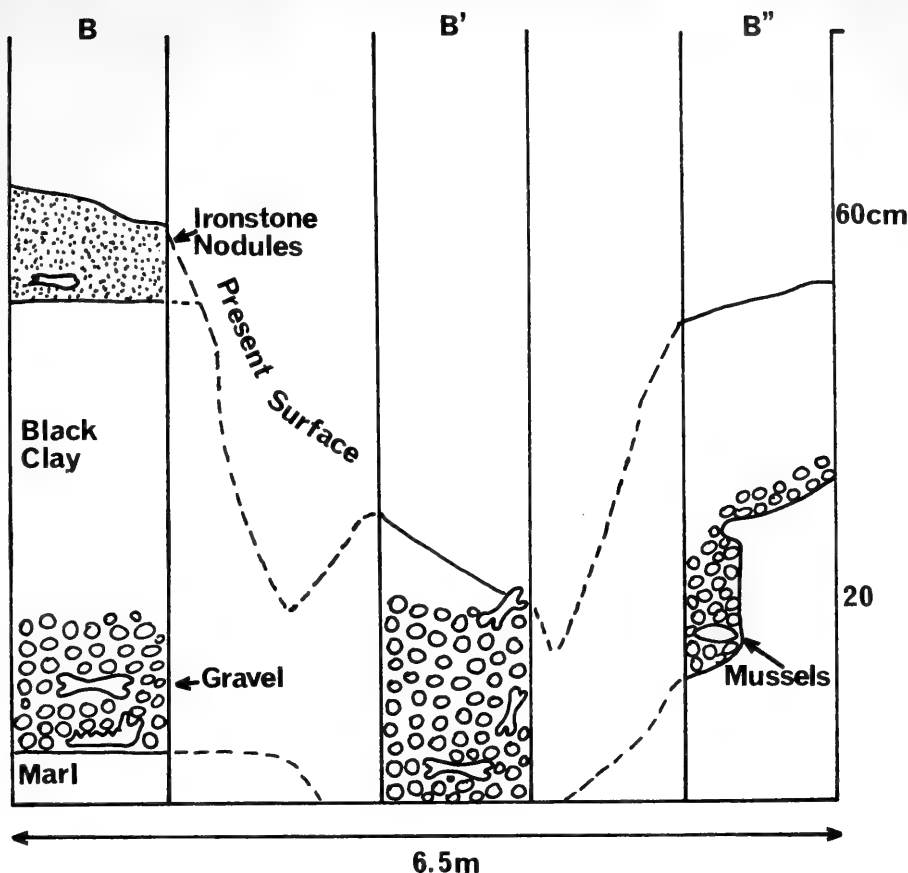


Fig. 4c. Section through site from B to B''. Near the base of the section in 4c the ledge of marl under which the *Velesunio* shells were found can be seen.

southwestern Victoria, at 142 25°E 38 00°S (Fig. 1). The fossil locality is located approximately 15 km downstream from the creek source and approximately 20 m downstream from a low (1 m) waterfall formed of tuff. In the immediate vicinity of the site, the creek meanders through a deep, broad valley, the surrounding hills being composed of a deeply weathered basalt mantled with small ironstone nodules (Figs 2-3). Below the fall, for a short distance, marine marls of Cheltenhamian age are exposed (Gill and Darragh 1963). The Pleistocene sediments rest unconformably on these marls.

The late Pleistocene sediments are divisible into three units. The basal layer is a gravel containing the teeth and bones of marine animals, phosphatic nodules, rare fragments of basalt, tuff fragments, small ironstone nodules and Pleistocene bones (clasts are mostly between 1-10 cm in length). All clasts except the basalt

fragments, ironstone nodules and Pleistocene bones are derived from the marine Tertiary sediments that crop out only in the immediate vicinity (within 30 metres) of the site. The presence of large clasts (apart from bone) derived almost solely from rocks exposed in the immediate area of the site suggests that the gravel represents an *in situ* erosional lag deposit rather than a fluvial deposit. The gravel may represent a short erosional episode. Basalt fragments derived from the surrounding hills are extremely rare in the gravel (although common in the creek today) and this may indicate impeded runoff from the surrounding hills, possibly caused by dense vegetational cover at least in the creek valley. In places where the gravel is thick enough for the clasts to touch, the gravel appears to be of a closed framework type. Isolated clasts are almost invariably resting on the basal marine marls and are enclosed in a black clay (see below). Many of the clasts are Pleistocene bones or bone fragments. In places, the gravel can be as much as 35 cm thick (in a small channel cut into the marine sediments), absent or only represented by rare isolated clasts.

Approximately 50cm of uniform, structureless, black, sticky clay overlays most isolated clasts where the gravel is thick enough (see Figs 4a, b and c). Plant material which is scattered throughout the clay shows no preferred orientation. Bones are extremely rare except at the base of the clay. The uniformity and lack of orientation of entombed particles in this clay suggests rapid deposition, although slower accumulation due to damming of the creek or stranding of a bend due to change in direction are possible. A further explanation (the one accepted here) for the origin of this clay may be a choking of the drainage by sediment transported from surrounding slopes following heavy rains after drought and/or fire had denuded the watershed. Many plant fragments (especially wood) from this layer are charred. A large fragment of wood from the base of the clay was charred on the upwards-facing side only. Freshwater mussels were found near the clay-gravel interface crowded under a ledge of marine marl in lifelike positions (Fig. 4c). They may have retreated under the ledge to aestivate and died as drought conditions worsened, or they may have been smothered by the rapid deposition of clay. There is thought to be no significant difference between the age of the gravel and the black clay because: 1, the bones show little signs of weathering and some are articulated, which indicates that they were probably quickly covered by the black clay; and, the underlying gravel appears to represent an erosion *in situ* lag deposit that is intimately commingled with the clay.

Above the black clay is a reddish mottled clay of uncertain thickness (slumping obscures its upper limit) which is rich in small ironstone nodules (0.5 to 1.0 cm in diameter) and which contains some bones and plant remains. This layer appears to represent an abrupt change in sedimentary regime but there is no evidence of an erosional surface separating the units. It is possible, however, that it represents a deep weathering profile. A further 2-3 m of black soil overlies the deposit, but slumping obscures precise sediment relationships.

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Plant remains (leaf, seed and stem fragments) from the base of the black clay have been dated using C14 at $19,800 \pm 390$ ybp (Teledyne isotopes 1-11,018). It is hoped that further dates can be obtained. While searching for large plant fragments, one of us (B.G.) noted that root penetration by modern plants was extremely rare, making contamination from this source unlikely.

Several factors support the hypothesis that the bones are contemporary with the dated plant remains. First, both are from the same stratigraphic horizon, being clasts in the base of the black clay or, in cases where the basal gravel is thick, in the gravel. Second, bone weathering data suggests that the bones were covered, presumably by the black clay and some plant matter, soon after decomposition of the carcasses. Thus even if all of the plant fragments were washed into the site with the black clay, the time difference for deposition would have been slight (perhaps less than a year). Third, the fact that several bones are articulated precludes the possibility that the bones were reworked from an older deposit.

ANALYSIS OF FLORA

The plant material analysed here was recovered from approximately 3300 gm of air dried clay collected from the base of the black clay unit, and was associated with a macropodine tibia (probably *Macropus giganteus titan*) that was removed from the site in a plaster jacket. The clay surrounding the tibia encased in the jacket supplied the material for this analysis.

Methods: Pieces of clay of approximately 200 gm were soaked for 2-3 hr in tap water, with occasional gentle stirring. This proved sufficient to disperse most of the clay. The resulting solution was then washed gently through sieves with 1.2, 0.5, 0.25 and 0.15 mm apertures; the sieved material was then dried at 95°C. and sorted under a 10X magnification. In all, approximately 2100 gm were treated, 1250 gm of matrix having been retained for reference. This report covers only the material from the 1.2 mm sieve.

Results. Tables 1-2 and 4 list plant materials identified. Table 3 lists the non-plant material found. Estimates of abundance were based when appropriate on intact plant organs.

Discussion. Two vegetational elements are present in the sample, one water associated and the other more typical of a water stress environment.

The water associated vegetation includes species of *Myriophyllum*, *Pimelea*, *Lilaeopsis*, *Villarsia*, *Juncus*, Cyperaceae, Caryophyllaceae and Polygonaceae. The size range of the fruitlets of *Myriophyllum* (1.5-2.5 mm long, mean 1.83 ± 0.25 mm; Table 5a) was represented by the following species: *M. salsugineum*, *M. porcatum* (both previously included in *M. elatinoides*; see Orchard 1981), *M. muelleri* and *M. latifolium*. *Myriophyllum latifolium* is at present confined to coastal districts of Queensland and northern New South Wales. Of the fruitlets found, 87% were smooth, which would identify them as either *M. salsugineum*

TABLE 1. Spring Creek plant remains, closely identified material.

Most closely corresponding modern plant	Nature of remains	Abundance (No. of specimens)
<i>Casuarina paludosa</i>	stem nodes and internodes, buds, flowers	abundant (121)
<i>Lilaeopsis polyantha</i>	fruit	rare (1)*
<i>Myriophyllum</i> spp.**	"seeds" (fruitlets)	abundant (127)
<i>Pimelea curviflora</i> , ssp. <i>gracilis</i> , var. <i>gracilis</i> (S. M. Threlfall, unpub.)	seeds	rare (7)
<i>Pimelea pauciflora</i>	seeds	frequent (68 + pieces)
<i>Stipa</i> sp.	awns, 0.3 mm. diam.	rare (2)*
<i>Villarsia</i> sp. (? <i>reniformis</i>)	seeds	rare (3)*

*Since these remains are close to or less than 1.2 mm diam., they may be more abundant in the fractions from the finer sieves, as yet unsorted; **See Table 5b for species possibly present.

TABLE 2. Spring Creek plant remains, generally identified material.

Identification	Nature of remains	Estimated No. species	Abundant (No. of specimens)
Leptophyllous dicots:*			
Epacridaceae	leaves	5	frequent (65)
Type	leaves	1	frequent (58)
others	leaves	17	abundant (161)
Cyperaceae and			
<i>Juncus</i> sp.	stems and stem bases	2	abundant
Monocots	leaf pieces		frequent
Woody dicot stems	stem pieces		occasional
Bark	bark flakes		occasional
Caryophyllaceae	seeds	1	rare (1)*
Polygonaceae			
(? <i>Rumex</i> sp.)	seeds	1	rare (7)*
Other seeds	seeds	30	frequent (76)
Moss	stem and leaf	1	rare (very fragile)

*Leptophyllous = leaves with areas less than 25mm² (Specht 1972).

or *M. muelleri* or both. Size distribution curves do not unequivocally indicate two populations of fruitlets, nor has the pollen of *M. muelleri*, which is distinctive, been found in the deposit. *Myriophyllum muelleri* is characteristic of still, shallow water (0.5 m) and is found sparsely in southern parts of western Victoria, Western and South Australia. *Myriophyllum salsugineum* is frequent in southern Victoria, southeastern South Australia including Kangaroo Island and in Tasmania,

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TABLE 3. Spring Creek remains, non-plant material.

Identification	Nature of remains	Abundance
Insects	exoskeleton fragments, faeces	occasional
Bone	small pieces	rare
Small marine molluscs	shells — from Miocene deposit	rare
Tuff	small lumps — Miocene deposit	occasional

TABLE 4. Spring Creek, preliminary pollen count. Some pollen counts have been made on the material from which the macro-plant remains were recovered, and the results are given in Table 4. The counts were done by Mrs Kathie Strickland, c/o Geography Dept. Monash University.

Pollen from Spring Creek deposit. Total of 5 slides		
Pollen	Number of grains	Remarks
<i>Casuarina</i> , app. 20 m	8	<i>C. paludosa</i> falls in this group.
app. 30 m	5	Includes <i>C. stricta</i> , <i>C. luehmanii</i> .
Chenopodiaceae	6	
Compositae, Tubiflorae	58	Includes tall shrubs of water's edge, as well as low herbs.
Epacridaceae	1	
<i>Halorhagis</i>	1	
<i>Hydrocotyle</i> ?	1	
<i>Leptospermum</i>	1	
Monolet fern spore	8	Not <i>Pteridium esculentum</i> .
<i>Myriophyllum</i>	2	These are not <i>M. muelleri</i> .
<i>Nothofagus</i>	1	
<i>Pimelea</i>	6	
<i>Plantago</i>	10	Low herbs.
Poaceae	3	

The total amount of pollen is very low, compared to a swamp or lake-bottom deposit; it is hoped that a core may be obtained from another part of the site which might yield a higher pollen count.

TABLE 5a. A comparison of fruitlets of *Myriophyllum* species.

Species	Length, mm	Surface
Spring Ck. deposit, 87%	1.83±0.25	smooth, dorsal line in some
Spring Ck. deposit, 13%	1.78±0.15	verrucose on ridges
<i>M. salsugineum</i> Orchard	2-2.5(-2.7)	smooth, faint dorsal line
<i>M. porcatum</i> Orchard	1.8-2.1(-2.5)	irregularly verrucose
		esp. on ridges
<i>M. muelleri</i>	1.5-2.0	smooth

TABLE 5b. A comparison of *Pimelea pauciflora* seeds with those recovered from the Spring Creek deposit.

	<i>Pimelea pauciflora</i>	Spring Creek seeds
No. intact seeds	14 (3 different plants)	62
Mean length mm	3.21 ± 0.39	3.25 ± 0.26
Mean width mm	1.97 ± 0.29	2.05 ± 0.20
Mean length/width	1.64 ± 0.14	1.59 ± 0.16

where it occurs at altitudes up to 1050 m. It is infrequent in the warmer parts of Vic., S.A. and W.A. In southeastern N.S.W. it is found at 1,200 m. It inhabits lakes and slow-flowing streams and will tolerate salt and calcareous waters (Orchard 1981). Of the species mentioned, it is the most cold resistant. Thirteen per cent of the fruitlets show bluntly conical projections that occur in longitudinal ridges thereby indicating them to be *M. porcatum*. This rare species is so far found only in two areas of Victoria — the northern Goulburn Valley and in temporary soaks in the Mallee, where it is able to survive on drying mud by producing roots along the stems (Orchard 1981), a structural capacity it shares with *M. salsugineum* (Aston 1977). As a result, these two species can survive summer drought.

Two *Pimelea* species are found in the deposit, *P. pauciflora* R. Br. (Fig. 5a, Table 5b) and *P. curviflora* ssp. *gracilis* var. *gracilis* (Fig. 5b). *Pimelea pauciflora*, the Poison Pimelea, is a slender shrub that grows to 3 m high. Its distribution extends from New South Wales (at higher elevations) to northern Tasmania. In Victoria it is a tall shrub along mountain streams in the east of the state, and although a single specimen was recorded from Skipton in western Victoria in 1861 (Threlfall 1982), that specimen had seeds which in no way conform to those of *P. pauciflora*. The species usually grows on stream banks (Curtis 1967), often in thickets (Burbidge and Gray 1976). Although it appears tolerant of low temperature, *P. pauciflora* requires a sheltered situation. In north-eastern New South Wales there is a very similar species, *P. neo-anglica*, which was once included with *P. pauciflora* (Beadle 1972, Jacobs and Pickard 1981; and, as *Pimelea* species C, Threlfall 1982). The seeds of the two species are indistinguishable but the ranges of the species do not overlap and we have assumed that the seed at Spring Creek belongs to the Victorian species. A Victorian species that most closely resembles the seed of *P. pauciflora* is the drought-resistant *P. microcephala*, which has a distinctly larger seed (5.0 mm.) and is found in very dry areas in the Mallee in western New South Wales, in Queensland and in South Australia. Figure 6 shows the Victorian distribution of *P. pauciflora*. The seeds have a succulent fruit coat that is poisonous to humans. Inside this is a large black stony testa (3.2 x 2.0 mm). This hard seed is the material found in the deposit. A single seed was recovered with part of the fruit coat still attached (Fig. 7) and, although some seeds show evidence of abrasion, this is not severe.

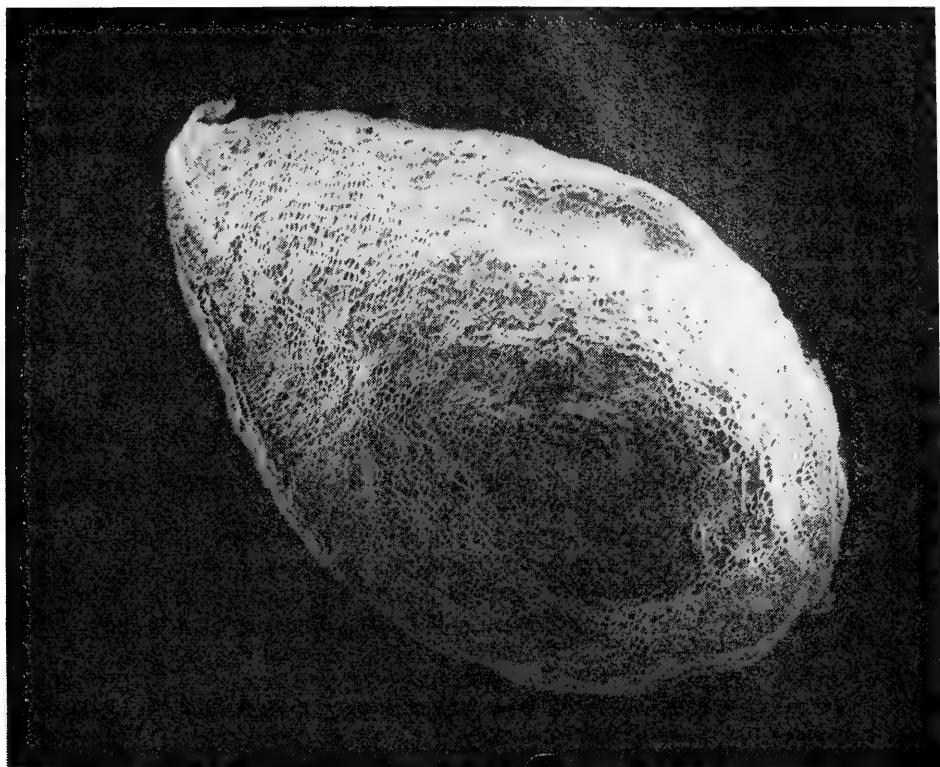


Fig. 5a. Seed of *Pimelea pauciflora* from Spring Creek.

Table 5a compares the dimensions of the fossil seeds with those of modern *P. pauciflora*. No other species of *Pimelea* except *P. neo-anglica* exhibits the same size, shape and surface sculpture.

Pimelea curviflora gracilis var. *gracilis* is a low undershrub. *Pimelea curviflora*, in the broad sense, exhibits a wide variability in seed size and sculpture, but the seeds recovered from Spring Creek correspond to the variety *gracilis* which occurs at high elevations in New South Wales and Victoria (700-1,200 m). There is a doubtful record from Portland, Victoria, about 60 km from Spring Creek. In South Australia it is recorded from a moist gully at Clarendon and in Tasmania it is found at lower altitudes amongst dense vegetation. Figure 8 shows its Victorian distribution. Neither the *Pimelea* nor *Myriophyllum* fruits show evidence of burning.

Lilaeopsis polyantha, *Villarsia* sp, Caryophyllaceae and Polygonaceae are all consistent with streamside or swampy habitats. Since all these seeds are small, more of them may be found in the fractions from the finer sieves. All are found

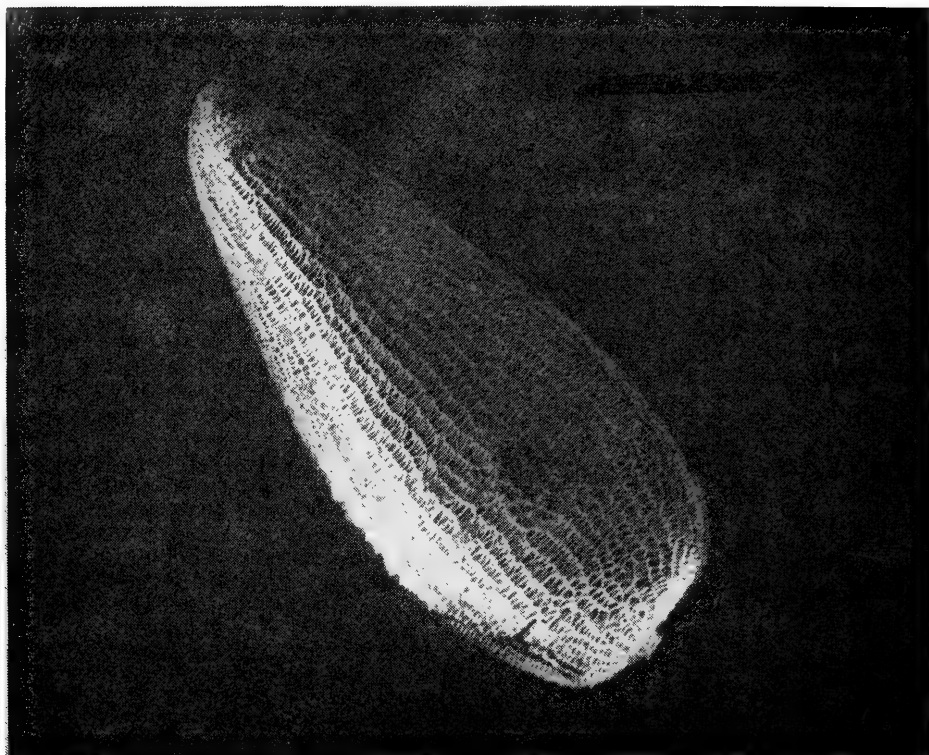


Fig. 5b. Seed of *Pimelea curviflora gracilis* var. *gracilis* from Spring Creek.

in the Western District at the present time. The stems and stem bases of Cyperaceae and *Juncus* spp., as well as the pieces of monocotyledonous leaves, are all of a relatively delicate nature and indicative of a wet habitat. Those members of these groups that inhabit dry environments are tough and hard.

Plants associated with a water stress environment include *Casuarina*, *Stipa* and other undetermined taxa characterised by leptophyllous leaves.

Casuarina paludosa, the Swamp Sheoak, is widespread in Victoria. It is a small erect shrub that grows to 1 m in height. It is a frequent component of coastal heaths (Willis 1972) but is also found in the Grampians and Big and Little Deserts. Although it can survive very dry conditions, it is often a component of wet heaths in Victoria, South Australia and northeastern Tasmania (Dodson and Wilson 1975, Kirkpatrick 1977). Despite their higher precipitation, these wet heaths represent a water stress environment for plants because of poor drainage (see below). Spring Creek falls into that area of the Western District that is characterised by soils of impeded drainage (Blackburn 1974). *Casuarina paludosa*

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Fig. 6. Distribution of *Pimelea pauciflora* in Victoria. X = Spring Creek.

occurs today at Kirkstall, about 35 km south of the site. Identification of the material as *C. paludosa* is based on vegetative characters — size, number of leaf teeth and the nature of the stem ridges (Fig. 9). While it is possible that some of the material could belong to *C. pusilla*, another dwarf species, the common western Victorian tree form, *C. stricta*, is not present.

A grass, *Stipa* sp., is represented by two pieces of stout awns. The stout-awned species of *Stipa* are found over a wide range of habitats. Even those of the alpine plains are subject to water stress.

The leptophyllous leaves, among which Epacridaceae are well-represented, suggest a water stress habitat even if it is presumed that small leaves have been preferentially preserved. No *Eucalyptus* remains have been found.

VEGETATION OF SPRING CREEK IN THE HISTORICAL PERIOD

Although the general description of the Spring Creek area was “volcanic plains”, this is now understood to have comprised a mixture of vegetation types — open forest, grassy plains and swamp (Willis 1972). Early accounts listed trees of *Eucalyptus viminalis*, *E. camaldulensis*, *E. ovata* (swamps), *Acacia melanoxylon*, *A. mearnsii*, *Exocarpos cupressiformis*, *Banksia marginata* and *Casuarina stricta*



Fig. 7. Seed of *Pimelea pauciflora* with seed coat, from Spring Creek.

in the immediate area (Bennett 1982, Presland 1977, Willis 1964, 1974). Even Mt. Rouse, where Spring Creek originates, was covered in trees. The creek was described in 1880 as a "... shallow drain passing through a sea of high rushes ..." (Bennett 1982). The term "rushes" would include species of *Phragmites* and *Typha* as well as Cyperaceae and Juncaceae. *Leptospermum* thickets bordered the streams and swampy areas. Most swampy areas were drained by settlers. In the case of some parts of Spring Creek, this was done by ploughing out the creek bed (Bennett 1982). Together with removal of the fringing vegetation, this led to greatly increased run-off, stream down-cutting and slumping of banks. *Themeda australis* (Kangaroo Grass) was abundant, giving way to tall tussock grass (*Poa labillardieri*) in wetter areas. Epacridaceae were probably poorly-represented (Willis 1964).

It can be seen that the 20,000 ybp period differs from the historical period in the absence of trees and the presence of *Pimelea pauciflora*, *Myriophyllum porcatum* and several epacrids.

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Fig. 8. Distribution of *Pimelia curviflora gracilis* var. *gracilis* in Victoria. X = Spring Creek site.

ENVIRONMENTAL RECONSTRUCTION

Watts (1978) has pointed out that an assemblage of plant fragments often “. . . does not appear to derive from any single, readily identified plant community . . .”, and it is important to “. . . consider the processes that have produced the assemblage”.

Firstly, both aquatic and water-edge plants would be expected to be present in the stream deposit. *Myriophyllum* will not fruit without free water at some period of the year but the water does not need to remain over the summer period. Even if the plant itself dies, the seeds can germinate when the water returns. Its presence suggests a slow-flowing stream or backwater and its fruits are unlikely to have been transported for a long distance since two fruitlets were found still adhering to one another. Its pollen also indicates a local presence.

Both species of *Pimelea* are found on streamside flats or on gravel banks subject to spring flooding. Their fruits are shed in late summer and lie on the ground below the bushes, not being swept away (in the case of *P. pauciflora* in its southern habitats) until the stream receives snow melt in spring. The succulent fruit coat has by then dried around the seed. In dry seasons, such as 1982 in Victoria, the fruits do not become succulent and tests using these dry fruits showed that they could float for up to 5 weeks if the coats were not

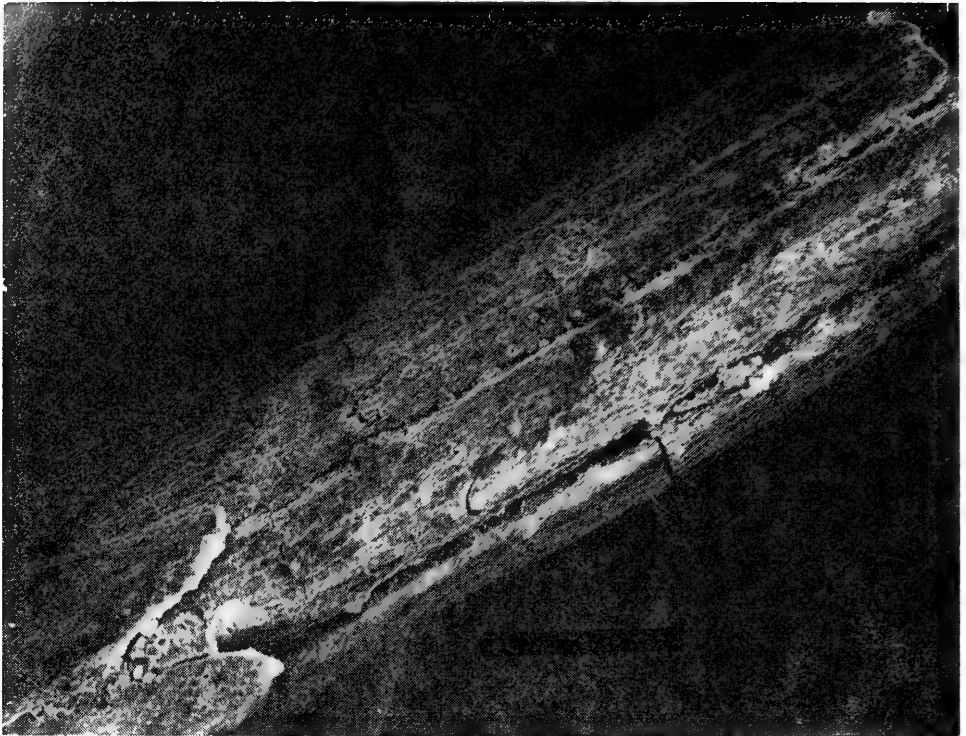


Fig. 9. Stem fragment of *Casuarina paludosa* from Spring Creek.

abraded. However, removal of the fruit coat can occur quite readily. In 1982, over 50% of the fruits collected from beneath one bush showed sufficient removal to expose the seed and, in these circumstances, flotation time did not exceed eight days. The toxicity of the fruit to animals other than Man is little-known, but the generally intact nature of the seeds in the deposit seems to exclude transport by birds or mammals. In general, the *Pimelea* seed probably had its origin quite close to the site of deposition. On the assumption that the morphological identity of the seeds in the deposit with *P. pauciflora* also indicates a physiological similarity, a sheltered stream-bed, dry in summer but possibly carrying snowmelt in the spring, seems a likely palaeoenvironment. Some parts of the stream-bed would certainly have held slow-flowing backwaters filled with, among other plants, species of Cyperaceae, Juncaceae and *Myriophyllum*.

Secondly, in the case of the "water stress" plants, these remains must have been carried into the stream by run-off from surrounding areas, possibly being carried some distance down the stream before being deposited. If the remains were carbonised by fire, as seems to have been the case with some, they could

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have floated for a considerable time. Runoff would favour the preservation of small intact leaves. Larger leaves such as those of eucalypts would be under-represented. *Eucalyptus* capsules might well be too large and too dense to be carried but leaf pieces and buds would be expected if there were any significant number of trees in the surrounding area; and no *Eucalyptus* pollen was found. There is only one possible epacrid fruit present, although epacrid leaves are plentiful. The absence of cones of *Casuarina* is less surprising, since they are relatively large and are retained on the plant.

The remains and diversity of species represented certainly suggest a low, heathy vegetation reasonably close to a stream. Heaths are found on nutrient-poor soil, either in deep sands or on soils with impeded drainage that are seasonally waterlogged and then subject to summer drought (Specht 1972). Alpine heaths occur both in well-drained and poorly-drained sites (Costin *et al.* 1979). Since there seem to have been no areas of deep sand close to Spring Creek at 20,000 ybp, wet heath seems more likely. It may seem a contradiction that a heath with seasonally waterlogged soil supports plants that show characteristics of water stress, but in these circumstances water absorption by the plant is difficult because of the poorly aerated soil. Another factor that greatly reduces the ability of the soil to supply water to the roots is low temperature; cold soil, even if the drainage is not impeded, will induce the same structural modifications in the plant as drought (Daubenmire 1974).

Watts (1978) has shown that macro plant remains tend to complement rather than confirm pollen analyses. This is because macro plant remains are less easily transported than pollen. Some pollens are carried over long distances from their place of origin, a notable example being the pollen of *Casuarina* species. The presence of pollen of tree species of *Casuarina* in the Spring Creek deposit, therefore, does not necessarily indicate a local presence. Other pollen is quite local in its dispersal, an example being that of Epacridaceae. As a result, the relative scarcity of this pollen does not necessarily contradict the evidence of the macro remains. The presence of large numbers of grains of the Compositae-Tubiflorae is not reflected in the macro remains. Perhaps this is because seeds of this group are small and not likely to preserve well. It is not possible to draw any useful conclusions from the presence of the pollen of Tubiflorae, because this group comprises about 270 native species, is widespread in every habitat, and contains small tree species as well as the very common aquatic plant *Cotula coronopifolia*, which grows today in Spring Creek.

Pollen counts from Wyrie Swamp, S.A., dated at 26,000 ybp (Dodson 1977), show a predominance of shrubby Casuarinas over tree types and a lower number of *Eucalyptus* compared to the postglacial period. By 16,000 ybp, *Casuarina stricta* (a tree) had become dominant. *Myriophyllum* was the most abundant aquatic pollen. Although this and other sites of comparable age at Hunter Island (Hope 1978) and Lancefield (Ladd 1981) are widely different

in geomorphology from Spring Creek, the overall picture is of reduced tree cover and low shrubby or grassy vegetation. It has so far not proven possible to obtain a satisfactory pollen core from the Spring Creek site. This would obviously be of great interest because pollen evidence from lowland sites in Victoria at the time of the glacial maximum is relatively scarce.

One of the difficulties of palaeoenvironmental reconstruction from plant remains is that it is the seasonal extremes rather than the average conditions which determine whether a species survives. One can only guess at which factors were most important in limiting tree growth 20,000 years ago. Lower precipitation might have been less important than increased evaporation due to lower humidity or stronger winds. The inability of the trees to extract sufficient moisture from cold or frozen soil also must have played a role.

In summary, the palaeobotanical data suggest that at the time of accumulation in the Spring Creek area, the vegetation was a low heath and that the creek valley provided shelter and seasonal water which, however, probably dried up in summer.

FAUNA

The only fossil material not collected by the author or associates from the Spring Creek site are two edentulous dentaries of *Macropus giganteus titan* and some bone fragments presented to the National Museum of Victoria by R.A.A. Applik in 1914. Their waterworn appearance indicates that they may have been collected some distance downstream from the site. They are not included in this analysis. All specimens are housed in the Museum of Victoria, Vertebrate Palaeontology collections (NMV).

Sixteen vertebrate taxa are known from the locality, twelve of which have been at least tentatively identified to species level (see Tables 6-8). The invertebrates from the site remain unstudied but include cf. *Velesunio ambiguus* (Hyriidae) and insects.

The most abundant vertebrates from the site are large mammals. Small vertebrates are rare, being represented by two murid incisors, a tibiotarsus identified as cf. *Tribonyx mortierii* (the Tasmanian Native Hen) and a fourth metatarsal of a small macropodine. Apart from these, the next smallest species is *Macropus agilis siva*. Modern specimens of *M. agilis* have an adult bodyweight of 7-9 kg (Main and Bakker 1982). Dental measurements of the fossil subspecies (*siva*) are 15-16% larger than those of the modern form (Marshall and Corruccini 1978). Attempts to sample by sieving at Spring Creek have been unsuccessful due to the nature of the clay. This may in part account for the paucity of small animals in the collections. However, small teeth and bone fragments of larger animals are common at the site (over 100 isolated teeth of *Macropus giganteus titan* have been found), indicating that if small species were well-represented, more specimens would have been found.

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TABLE 6. Dental dimensions of *M. giganteus titan*, from Spring Creek. M = mean, L = length, W = width, O.R. = range, N = number.

II/ M	= 7.5	O.R. = 6.4-8.6,	N = 6			
I2/ M	= 7.6	O.R. = 7.1-8.1	N = 2			
I3/ M	= 16.5	O.R. = 15.8-17.6	N = 3			
P2/ M.L.	= 9.3	O.R. = 9.3	N = 2	M.W. = 7.2	O.R. = 7.0-7.4	N = 2
P2/ M.L.	= 8.2	O.R. = 8.1-8.3	N = 4	M.W. = 4.6	O.R. = 4.1-5.0	N = 4
P3/ M.L.	= 9.8	O.R. = 8.7-10.5	N = 7	M.W. = 5.4	O.R. = 4.8-5.7	N = 7
P3/ M.L.	= 7.5		N = 1	M.W. = 3.9		N = 1
M1/ M.L.	= 11.0	O.R. = 11.0	N = 2	M.W. = 8.6	O.R. = 8.3-8.9	N = 2
M2/ M.L.	= 12.4	O.R. = 11.8-12.8	N = 4	M.W. = 10.1	O.R. = 9.4-11.2	N = 4
M3/ M.L.	= 14.1	O.R. = 12.7-15.5	N = 3	M.W. = 11.4	O.R. = 10.4-12.5	N = 3
M4/ M.L.	= 15.7	O.R. = 14.8-17.0	N = 4	M.W. = 11.9	O.R. = 10.9-12.7	N = 4
M5/ M.L.	= 17.1	O.R. = 15.1-18.1	N = 4	M.W. = 12.7	O.R. = 11.5-13.5	N = 4
M1/ M.L.	= 10.6	O.R. = 10.0-11.0	N = 5	M.W. = 6.9	O.R. = 6.8-7.0	N = 5
M2/ M.L.	= 12.1	O.R. = 10.6-13.2	N = 9	M.W. = 8.0	O.R. = 7.7-8.2	N = 9
M3/ M.L.	= 14.6	O.R. = 13.0-15.6	N = 10	M.W. = 8.0	O.R. = 7.7-8.2	N = 9
M4/ M.L.	= 16.0	O.R. = 14.3-17.4	N = 19	M.W. = 10.1	O.R. = 9.3-10.6	N = 19
M5/ M.L.	= 17.4	O.R. = 16.1-18.6	N = 21	M.W. = 10.2	O.R. = 9.1-10.8	N = 19

Just as *Macropus agilis* is represented by a slightly larger form than the modern one at late Pleistocene localities, so is *M. giganteus*, specimens from the site having teeth 26% larger on average than a modern sample of *M. giganteus* from Victoria (Flannery 1981, and see Table 6). In the past, this large form of *M. giganteus* has been named *M. titan* but there does not seem to be sufficient justification to maintain this distinction (Flannery 1980, 1981). Here it is given subspecific distinction as *M. giganteus titan*. No individuals the size of modern specimens have been recovered from Spring Creek. *Macropus* (*Osphranter*) *rufus* specimens from the site fall within the size range observed in the modern population and clearly do not represent a gigantic form. *Macropus* (*O.*) *rufus* is represented only by pedal remains but these are distinctive, showing a marked distal dorsoventral compression of the fourth metatarsal (a derived feature seen

TABLE 7. Dental measurements of mammal species other than *Macropus giganteus titan* from Spring Creek. Measurements in mm. l = length, w = width, R = right side, L = left side.

<i>Diprotodon</i> sp.									
N.M.V.	P157312	L	M/5	l=40.2					
<i>Zygomaturus trilobus</i>									
N.M.V.	P157315	L	M/5	l=51.8	w=34.8				
N.M.V.	P157314	R	M2/	l=36.5					
N.M.V.	P157313	R	P3/	l=51.8	w=34.8	M2/ l=33.8	w=31.8	M3/ l=42.1	w=35.3
			M4/	l=48.1	w=40.7				
<i>Palorchestes azael</i>									
N.M.V.	P157320	L	M/5	l=30.7	w=19.0				
<i>Protemnodon</i> sp. cf. <i>P. anak</i>									
N.M.V.	P157293	R	P/3	l=16.2	w= 5.8				
<i>Protemnodon</i> sp. cf. <i>P. brehus</i>									
N.M.V.	P42526	R	P/3	l=15.8	w= 7.7	M/2 l=10.6	w= 9.6	M/3 l=13.5	w=11.6
			M/4	l=16.7	w=12.4	M/5 l=18.7	w=13.1		
N.M.V.	P42526	L	P3/	l=19.2	w=10.6	M2/ l=11.4	w=12.6	M3/ l=14.9	w=13.0
			M4/	l=16.6	w=14.0	M5. l=16.9	w=14.2		
N.M.V.	P42526	R	P3/	l=19.1	w=10.4	M2/ l=11.0	w=12.8	M3/ l=14.6	w=13.4
			M4/	l=17.0		M5/ l=17.0			
<i>Simosthenurus</i> sp. cf. <i>S. occidentalis</i>									
N.M.V.	P157301	L	P/3		w=10.5	M/2 l=12.3	w=11.5	M/3 l=13.9	w=12.6
			M/4	l=15.2	w=12.8	M/5 l=15.2	w=12.5		
<i>Sthenurus andersoni</i>									
N.M.V.	P159934	R	P/3	l=15.4	w= 8.1	M/1 l=10.0		M/2 l=11.3	w= 9.5
			M/3	l=12.0	w=10.8	M/4 l=12.8	w=11.7	M/5 l=13.4	w=11.8
N.M.V.	P157295	R	P/3	l=13.7	w= 7.7	M/2 l=10.1	w= 9.4		
<i>Simosthenurus gilli</i>									
N.M.V.	P157296	R	P/3	l=14.8	w= 8.7	M/2 l= 8.9	w= 7.9	M/3 l=10.0	
N.M.V.	P157297	L	P/2	l= 9.5	w= 7.7				
N.M.V.	P157294	R	M/2	l= 9.1		M/3 l=10.5	w= 9.0	M/4 l=10.8	w= 9.4
			M/5	l=10.3	w= 9.2				
N.M.V.	P157294	L	M/2	l= 9.1	w= 8.4	M/3 l=10.4	w= 9.6	M/4 l=10.8	w= 9.4
<i>Macropus agilis siva</i>									
N.M.V.	P157388	R	M/3	l= 8.7		M/4 l=10.5	w= 7.0	M/5 l=11.5	w= 7.0
N.M.V.	P157304	R	M/2	l= 8.8	w= 5.5	M/3 l=10.4	w= 5.9		
N.M.V.	P157306	L	M/4	l= 9.1		M/5 l=11.2	w= 8.0		
N.M.V.	P157303	R	P/3	l= 9.0	w= 3.6	M/2 l= 9.0	w= 5.9	M/3 l=10.8	w= 6.4
N.M.V.	P157305	L	P/3	l= 9.0	w= 3.4	M/2 l= 8.2	w= 5.8	M/3 l= 9.9	w= 6.4
N.M.V.	P157302	L	P/3	l= 8.1	w= 3.9	M/3 l= 8.9	w= 6.3	M/4 l=10.5	w= 7.0
			M/5	l=11.8	w= 7.1	Jaw diastema	=44.4		
N.M.V.	P157302	L	P/3	l=10.0	w= 5.3	M/3 l= 9.7	w= 7.6	M/4 l=11.6	w= 8.2
			M5/	l=12.9	w= 8.5				
N.M.V.	P157302	R	P3/	l=10.1	w= 5.0	M3/ l=10.0	w= 7.5	M4/ l=11.7	w= 8.1
			M/5	l=12.9	w= 8.5				

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TABLE 8. Vertebrate species found at the Spring Creek Site. * = extinct.

Taxa	Minimum number	Species	% of Total	Family
MACROPODIDAE				76.8
<i>Macropus giganteus titan</i>	18	43.0		
<i>Macropus agilis siva</i>	5	11.6		
* <i>Simosthenurus gilli</i>	4	9.3		
<i>Macropus rufus</i>	2	4.7		
* <i>Protemnodon</i> sp. cf. <i>P. brehus</i>	1	2.3		
* <i>Protemnodon</i> sp. cf. <i>P. anak</i>	1	2.3		
* <i>Simosthenurus</i> sp. cf. <i>S. occidentalis</i>	1	2.3		
* <i>Sthenurus andersoni</i>	1			
MACROPODINE INDET.	1	2.3		
DIPROTODONTIDAE				7.0
* <i>Diprotodon</i> sp.	1	2.3		
* <i>Zygomaturus trilobus</i>	2	4.7		
PALORCHESTIDAE				2.3
* <i>Palorchestes azael</i>	1	2.3		
THYLACOLEONIDAE				4.7
* <i>Thylacoleo carnifex</i>	2	4.7		
DASYURIDAE				2.3
cf. <i>Sarcophilus</i>	1	2.3		
MURIDAE	1	2.3		2.3
AVES				2.3
cf. <i>Tribonyx morterii</i>	1	2.3		

in all *M. (Osphranter)* with the same element being elongate and possessing a rounded dorsal surface (as in *M. (O.) rufus*, see Fig. 10). NMV P159935 consists of the articulated metatarsals 2-5 of *M. (O.) rufus* and shows the thin fifth metatarsal also typical of the species of *M. (Osphranter)*, in particular *M. (O.) rufus*.

Identification of *Protemnodon* sp. cf. *P. brehus* (see Figs. 11-12) has presented some problems. While conforming to the diagnosis of the species provided by Bartholomai (1973) in most features, the Spring Creek specimen differs in possessing un-retracted nasals such as occur in *P. anak*. Bartholomai suggests, on the basis of specimens from Lake Tandou and the Darling Downs, that *P. brehus* has retracted nasals (as does *P. roechus*). The Spring Creek specimen is tentatively referred to *P. brehus*, pending a future revision of the genus.

Macropus giganteus, an extant species, is by far the most common mammal present at the Spring Creek site, making up 42% of the minimum number of individuals recovered. It is also the only species collected at the fossil site known to have inhabited the area in historic times (Bennett 1982). The next most



Fig. 10. Fourth metatarsal of *Macropus (Osphranter) rufus* P157288 from Spring Creek.

common species, *M. agilis*, is also extant. Only two other extant species are present, *M. (O.) rufus* and *Tribonyx mortierii* (tentatively identified). Because these species are the only ones likely to provide reliable palaeoenvironmental data, their habitat preferences will be discussed here.

Modern *M. giganteus* occurs in a wide variety of habitats, from the semi-arid land east of Broken Hill to the wet sclerophyll forests of the dividing ranges of eastern Australia (see Fig. 13). It is usually found in woodland and forest areas (Frith and Calaby 1969) but can survive in open grassland (see Bennett 1982). With such a wide tolerance of habitat, *M. giganteus* is not particularly useful for palaeoenvironmental interpretation.



Fig. 11. Stereo pair of occlusal view of *Protemnodon* sp. cf. *P. brehus* dentary P42526.

Modern *M. agilis* lives in tropical Australia, extending only as far south as Stradbroke Island on the east coast. Troughton (1973, p169) notes that it inhabits "... suitable scrub and long grass country ... supplied with occasional streams ...". The subspecies *M. a. siva* (Fig. 14) must have had different habitat requirements than the living forms because it is found as far south as Victoria in fossil sites that accumulated at a time when temperatures were considerably lower than they are at present. In view of this, it seems unsafe to base palaeoenvironmental interpretations on this species.

Macropus (*O.*) *rufus* occurs today in the arid inland of Australia with most of its range within the 38 cm (15") rainfall isohyet (Newsome 1977, and Fig.

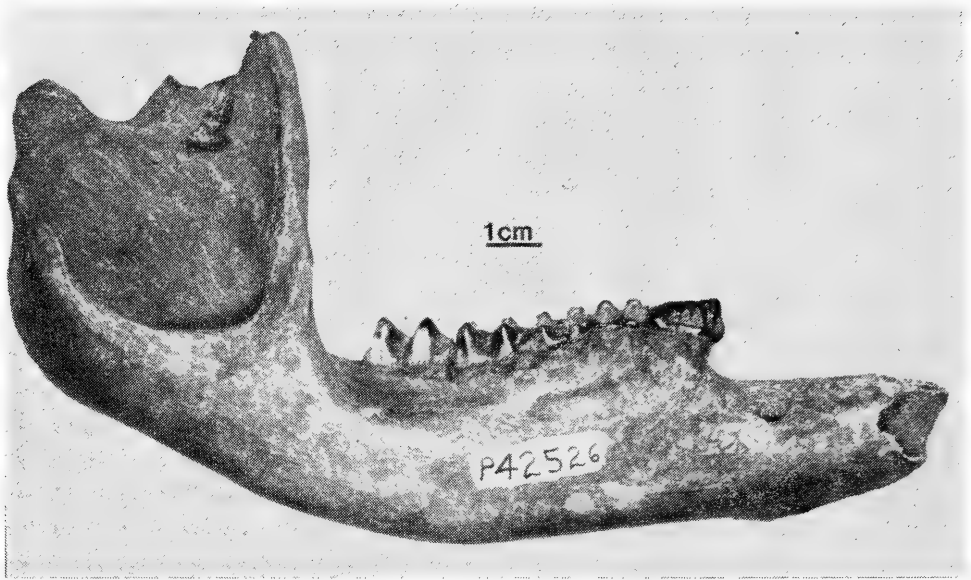


Fig. 12. Buccal view of left dentary of P42526, *Protomnodon* sp. cf. *P. brehus*.

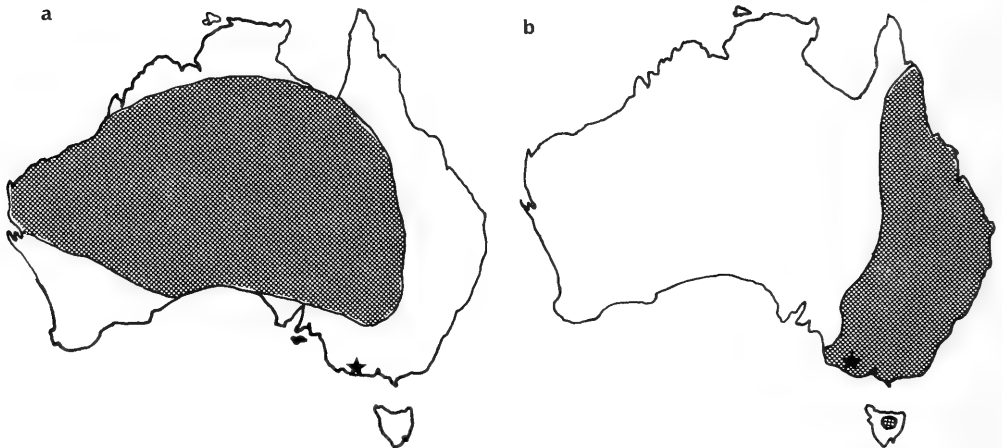


Fig. 13. Distribution of (a) *Macropus (Osphranter) rufus* (from Frith and Calaby 1969); (b) *Macropus giganteus* from Frith and Calaby 1969).

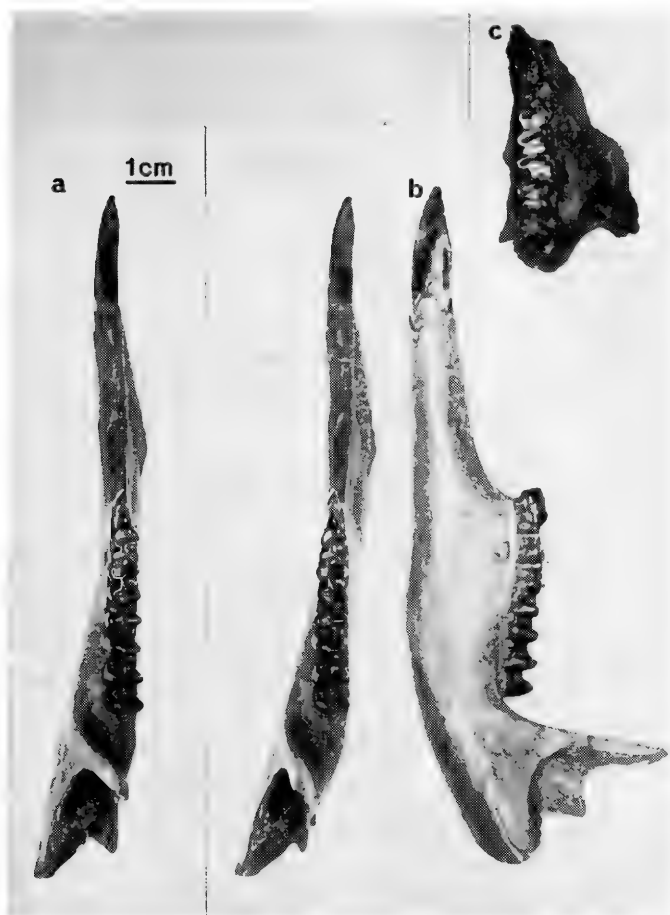


Fig. 14. (A) stereo pair, and (B) lingual view of *Macropus agilis siva* dentary NMV P157302. (C) occlusal view of maxilla of same individual.

13). Its present distribution suggests that it is highly tolerant of hot, dry conditions and that it prefers open space to woodland. Penshurst, approximately 15 km northwest of the site, receives an average of 71.8 cm rainfall annually (in the 92 years to 1980). No topographic features are present that would significantly alter the rainfall of the Spring Creek site from that of Penshurst. In conjunction with climatic data presented in Bowler *et al.* (1976), the presence of *M. (O.) rufus* at Spring Creek probably indicates drier conditions in the Western District at around 20,000 ybp than occur in this area at present.

Tribonyx mortierii is today restricted to Tasmania, although its fossil remains have been found as far north as Queensland (Olson 1975 and Fig. 15). In



Fig. 15. Distribution of *Tribonyx mortierii*. Stars = some fossil occurrences.

Tasmania, it is found around swamps and creeks, especially where both scrub and open sward are present, at altitudes up to 900 m (Ridpath and Moreau 1966, Ridpath 1972). The apparent presence of this species may be a further indication of formerly dense vegetation in the creek valley with some open areas nearby.

The palaeoecology of the totally extinct species found at Spring Creek is poorly-known. However, the site contains both *Zygomaturus trilobus* and *Diprotodon* sp., which Hope (1982) has suggested are predominantly coastal (former) and inland (latter) forms. On this basis, it appears that Spring Creek may have been near the interface of coastal and inland zones and that, during a drought, water may have attracted species to the area which otherwise did not occur there.

TAPHONOMY

Taphonomic studies of the Spring Creek site were undertaken because it was felt that they might yield data relevant to the understanding of megafaunal extinction. Bone orientation data were collected at Spring Creek mainly for bones collected during 1980-81, although data was recorded for approximately 10 bones from an earlier dig. Data were not collected for bone fragments less than 5 cm long. Most bones were found concentrated around a small channel trending NE-SW (see Fig. 4). While data points are few, there appears to be a weak NE-SW preferred orientation for the long axes of bones (Fig. 16). This may suggest a very weak water-caused alignment of bone fragments.

Many more large elements and associated or articulated bones have been found in or near the south bank of the creek (e.g., NMV P157249, NMV P42526) than in the north, indicating that the proximal end of the bone accumulation is in the southwestern part of the deposit, most of which remains unexcavated. Bones

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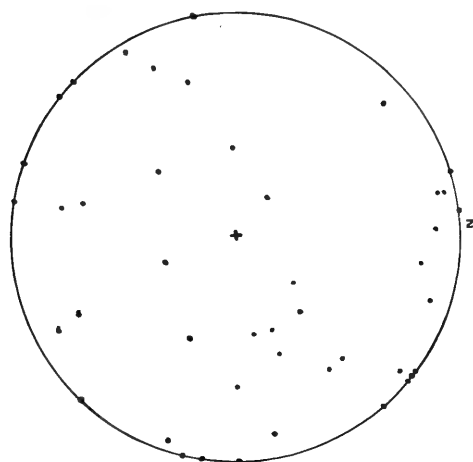


Fig. 16. Orientation of long axes of elongate bones plotted on lower hemisphere projection.



Fig. 17. Clavicle of large macropodid showing paired cut marks attributed to *Thylacoleo*.

rapidly become scarce towards the north bank, being very rare more than 5 m northeast of the survey peg in the southwest bank. While less well-defined, the channel seems to continue in this direction. The relationship of the small number of bones found along the north bank of the north channel (including NMV P157294, NMV P157295 and NMV P157320) to the bones in the main accumulation is not known. Stratigraphically there is no reason to suspect a different age for these bones. For taxonomic and other purposes they were included with the main collection from the gravel and base of the clay.

Many bones from the site have been examined for surface weathering features and have been classified according to the six stage system of Behrensmeyer (1978). Bones not included in this analysis are those not found in situ, small fragments (less than 5 cm long) or bones whose surfaces are obscured. In all, 174 bones and fragments were included in the analysis: 83.3% fall into Stage 1 or 0 (with some bones showing stage 1 wear on one side and Stage 0 on the other); 12.6% fall into stage 2; 4% into stage 3; and none into stages 4 and 5. Because the vast majority of the bones examined fall into stage 0 and 1, it appears that nearly all the bones had been exposed to the atmosphere for a similar length of time. The bones are not greatly weathered which suggests that they were exposed subaerially for only a short time.

Although many bones are broken, most breaks have sharp edges. Bones may have been broken by scavenging (see below) or by trampling by other animals attempting to reach water. Some bones exhibit elongate, paired cut marks (see Fig. 17). Horton and Wright (1981) have examined similar marks on bones from Lancefield and conclude that the cuts were most likely made by the Marsupian Lion, *Thylacoleo carnifex*. Of the post-cranial elements and scraps collected, 3.8% showed paired cut marks attributable to *T. carnifex*. This is a conservative estimate of the number of bones with such marks because many fragments represent only one side of a bone and so could not preserve paired marks. Of macropodine postcranial bones (usually complete), 11% showed cut marks. *Thylacoleo carnifex* may have killed animals attracted to water and/or scavenged carcasses. Only 0.35% of the bones from Lancefield display tooth marks similar to those discussed above (Gillespie *et al.* 1978). This may be because the bones were more accessible at Spring Creek than at Lancefield or because *T. carnifex* was more abundant at Spring Creek.

AGE STRUCTURE

Interpretation of the age structure of fossil mammal assemblages can potentially yield much information. However, care must be taken to ensure that differential destruction of a particular age class or size of bones has not biased the age structure of a sample. *Macropus giganteus titan* is the most abundant animal at Spring Creek and is the only species well enough represented to analyse age structure in detail. The age of the dentaries in the sample was determined by examination of molar eruption and progression as outlined in Kirppatrik (1965).

SPRING CREEK MEGAFaUNAL ASSEMBLAGE

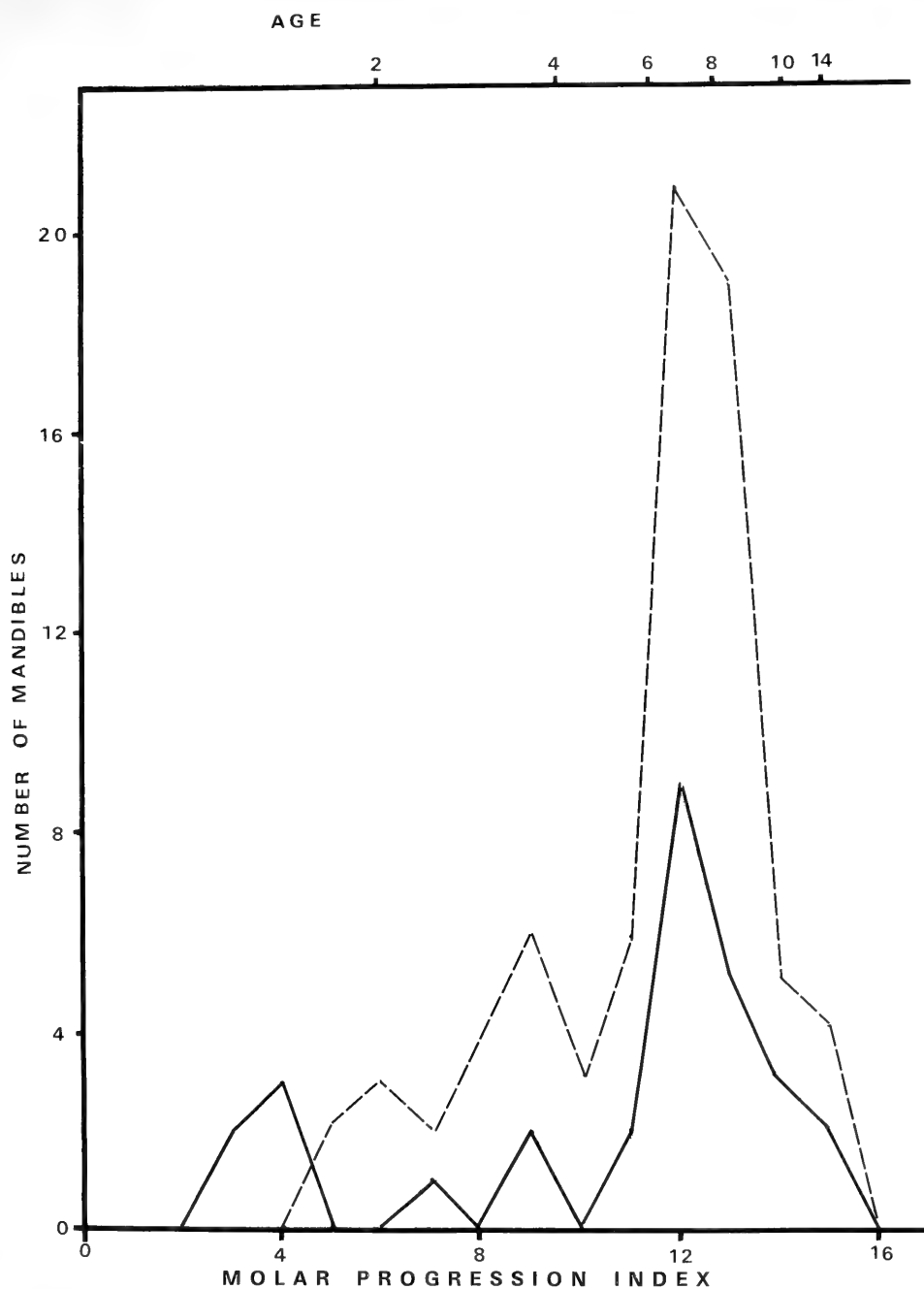


Fig. 18. Age frequency distribution of *Macropus giganteus titan* from Lancefield, Victoria (from Gillespie *et al.* 1978, dashed line) and from Spring Creek, Victoria (solid line).

The age structure is very similar to that seen in the Lancefield sample of *M. g. titan* (Gillespie *et al.* 1978, Horton 1976). In both, juveniles are conspicuous by their rarity (Fig. 18). This differs greatly from age structures noted by Wells (1978) for *M. rufogriseus* from Victoria Fossil Cave, South Australia and by Voorhies (1969) for fossil Holarctic herbivores (Fig. 19).

To determine if the rarity of juvenile dentaries at Spring Creek is due to their differential destruction, numbers of isolated teeth and the condition of the dentaries were examined. The likely position of isolated molars in the tooth row was determined by size. No M/1's, only 3 each of M/2 and M/3, 8 M/4's and 5 M/5's were found. Clearly, anterior molars (the ones usually found in juvenile dentaries) are not disproportionately represented.

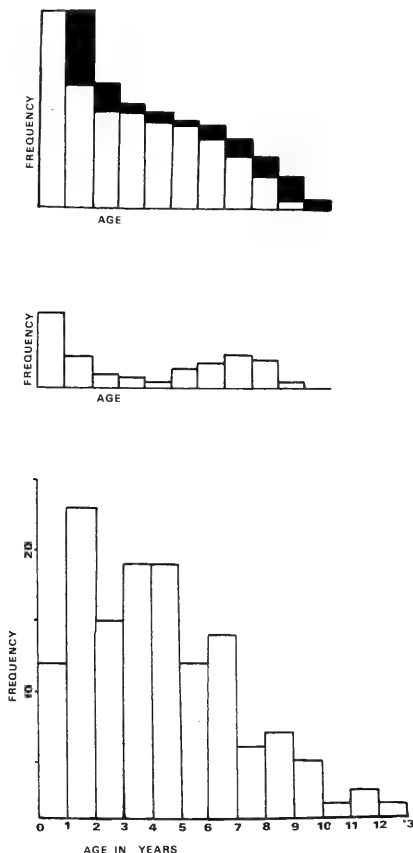


Fig. 19. Top: theoretical age distribution of a living population of ungulates with a potential longevity of 11-12 years. Middle: age distribution of a fossil population abstracted from living population by attritional mortality (from Voorhies 1969). Bottom: age frequency distribution of a fossil population of Red-neck Wallabies *Macropus rufogriseus* from Victoria Cave, South Australia (from Wells 1978).

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TABLE 9. Herbivore taxa (excluding *M. giganteus titan*) from Spring Creek arranged from top to bottom in order of decreasing body size. Column one lists a minimum number of individuals where at least some molars are or are estimated to be unworn. Column 2 lists individuals where all molars are or are estimated to be worn. * = taxon extinct.

	Column 1	Column 2
<i>Diprotodon</i> sp *		1
<i>Zygomaturus trilobus</i> *		2
<i>Palorchestes azael</i> *		1
<i>Protemnodon</i> sp. cf. <i>P. brehus</i> *		1
<i>Simosthenurus</i> sp. cf. <i>S. occidentalis</i>		2
<i>Sthenurus andersoni</i> *		1
<i>Macropus rufus</i> (based on pedal remains)	1	1
<i>Simosthenurus gilli</i> *	1	2
<i>Macropus agilis siva</i>	2	3

Dentary completeness was also estimated on the basis of completeness of the diastema (a structure often broken in fossil dentaries). If juvenile dentaries were being differentially destroyed, one would expect them to be in worse condition than the dentaries of adults. Of dentaries of animals less than two years old, 40% had complete diastemas, as did (approximately) those animals over two years old. Dentaries not found in situ were excluded.

It is possible that juvenile bones could be removed from a deposit by current action strong enough to move small, light bones but not larger, heavier ones. If this was the case at Spring Creek, one would expect small bones to be under-represented and scattered over a large area. Small bones, and particularly isolated teeth, are relatively common in the deposit, as are small fragments of larger bones. The limited area over which the bones have been spread, the geological data and the lack of preferred orientation of the long axes of bones suggest sluggish water flow. Also, the young of much larger animals than *M. g. titan* are totally absent from the deposit, a fact that cannot be explained by water sorting of bones. On the basis of these data, it appears unlikely that juvenile dentaries have been differentially destroyed or removed from the deposit.

Despite small sample sizes, an attempt has been made to estimate the ages of herbivores other than *M. g. titan* from Spring Creek. As with *M. g. titan*, juveniles overall are rare (Table 9). In Table 9, species are arranged in order of descending body size. Because many specimens are fragmentary, often the only estimate of age that could be used was whether or not all molars were worn. In specimens where the tooth row was incomplete, comparison was made with more complete specimens from other localities and molar wear estimated. *Macropus* (*O.*) *rufus* is known only from pedal remains at Spring Creek. However, one specimen is from a very young animal (with unfused epiphyses) while the other is clearly from an adult. For convenience, the juvenile has been placed in column 1 and the adult in column 2 of Table 9. As can be seen in Table 9, no juveniles

were found in species estimated to be larger than *M. (O.) rufus*, which average 42 kg for males and 22 kg for females according to Main and Bakker (1982). All larger forms, except *M. giganteus* are also extinct. Of species smaller than *O. rufus*, only one is extinct and juveniles are present in the sample.

DISCUSSION

Data collected from the Spring Creek site has allowed us to reconstruct the environment of the area at the time of deposition, estimate the age of the deposit and to speculate on factors that contributed to the bone accumulation.

Spring Creek has shown that a diverse megafaunal assemblage existed in southwestern Victoria until at least 20,000 ybp. It also provides the youngest reliable dates for *Thylacoleo carnifex*, *Palorchestes azael*, *Simosthenurus occidentalis*, *Sthenurus andersoni*, *Protemnodon anak* and *Protemnodon* sp. cf. *P. brehus*. With the Rocky River locality (J. Hope pers. comm.), it provides the most recent records of *Zygomaturus* and *Diprotodon* species. Although *Homo sapiens* is known to have been present in Australia more than 20,000 ybp, the site has yielded no sign of Humans.

The age of the Spring Creek site is of particular interest because few Australian sites containing megafaunal elements are as young as 25-15,000 ybp. Examples of sites that include Clogg's Cave (Flood 1973), Seton rockshelter (Hope *et al.* 1977) and Lancefield Swamp (Gillespie *et al.* 1978). Lancefield swamp, dated around 25,000 ybp, approximately 200 km east of Spring Creek, is one of the better documented localities. It shows many points of similarity with Spring Creek. Both are open (rather than cave) sites and have a similar mammalian fauna containing *Diprotodon* sp, *Macropus giganteus titan*, *Protemnodon anak*, *P. brehus* and *Simosthenurus occidentalis*. The age structure of the *M. g. titan* samples from both sites is similar and vegetation studies for both sites indicate a lack of trees.

Much information relating to climate has been gathered from the Spring Creek site. It supports other studies (e.g. Bowler *et al.* 1976) that indicate that southwestern Victoria was colder and drier than at present at around the height of the last southeastern Australian glaciation. Several species that are widely separated today co-existed in the area at that time. Examples are *Macropus (Osphranter) rufus* and *Pimelea pauciflora*. At present, the former inhabits the arid inland plains while the latter is restricted to streamside mountain areas. Voorthies (1969) notes similar species pairs that, although allopatric at present, are found together in fossil localities in the United States. He interprets this to mean that they must have been transported from different habitats. These anomalous associations are interpreted in a different way here. There is little possibility of reworking or of long distance transport into the site for *Pimelea* or *Macropus (Osphranter)* (see above). Also, these species are separated by hundreds of kilometers at present and several intermediate vegetation zones. The most likely explanation is that the species were in fact sympatric, but that climatic change or other ecological factors have

since restricted both species' ranges. Another study of anomalous species associations in Australian fossil deposits has been carried out by Lundelius (1983), and this is one of the options considered by him. The factors that restrict the distribution of these forms may be relatively simple ones. For instance, although high summer temperatures may restrict *P. pauciflora* to high altitudes in Victoria it can reach lower altitudes in Tasmania because the summers are cooler. Most of the present range of *M. (O.) rufus* is contained within the 38 cm rainfall isohyet. It may be restricted by the vegetational changes that accompany higher rainfall, or by competition with species from higher rainfall areas. If, during the height of the last glaciation in southeastern Australia, conditions were colder by up to 10° C (Bowler *et al.* 1976) and drier than at present, the factors that now determine the ranges of these species may have been relaxed, allowing them to occupy much larger ranges and to become sympatric. Palaeoecological interpretation of late Pleistocene faunas may be complicated by such conditions.

Our overall palaeoecological interpretation of the site is as follows. Topographically it would have been similar to the present, although the creek may have flowed only seasonally and would have meandered over a slightly different course in the valley floor. The area would probably have been treeless. A wet heath would have existed at least on the valley floor. Not all of the vertebrates found at the site would necessarily have lived in this habitat. Large mammals can travel a considerable distance to reach water and drought may have drawn animals from diverse and distant habitats. Species such as *Tribonyx mortierii*, however, were probably inhabitants of the immediate vicinity because the habitat envisaged is similar to that to which this species is found in at present. *Tribonyx mortierii*, being small and flightless, probably would not have travelled far particularly in open country.

The bone accumulation. Several factors may explain the origin of the Spring Creek bone accumulation. These fall into two basic categories. Either the bones represent an attritional accumulation (such as an accumulation of bones scoured from a wide area of countryside during a flood) or a catastrophic one (such as mass death by bogging, poisoning, drought or some other cause). The likelihood that the bones represent an attritional accumulation is lessened by the low degree of bone-weathering observed. Most bones fall into one or two classes in respect to bone-weathering, suggesting that they had been exposed to the atmosphere for a similar short period of time and thus that death of the animals was more or less simultaneous. That the bones are sometimes found articulated, scattered over a very small area and are poorly-sorted suggest that waterflow was sluggish and that the bones had not travelled far. Thus they have not been scoured from a large area by a flood. More likely the bone accumulation represents a catastrophic event.

The possibility that the bone accumulation resulted from a mass bogging is unlikely for several reasons. Firstly, there is no bog known in the area and the geology of the immediate area is now, and was probably in the Pleistocene, unsuit-

able for the development of bogs. Secondly, many bones (including foot elements) have been scavenged, indicating exposure when soft tissues were present. While poisoning is another possibility, neither this explanation nor the bog hypothesis can account for the lack of juvenile marsupials in the fossil sample.

The possibility that the Spring Creek bone accumulation resulted from a drought-killed population, however, is supported by several lines of evidence. The age structure of the *Macropus giganteus titan* sample differs from both attritionally and catastrophically accumulated samples of placental herbivores examined in Voorhies (1969) and for the catastrophically accumulated sample of *M. rufogriseus* cited in Wells (1978). However, it is similar to the *M. g. titan* sample from Lancefield, Victoria analysed by Gillespie *et al.* (1978). Gillespie *et al.* give two alternative explanations for the age structure: either only adults in a normal population were dying, or few juveniles were present in the population at the time of death. Given the lack of evidence to support the first hypothesis, and abundant evidence for the second (see below), the second seems more likely. Newsome (1977) notes that large gaps can be expected in the age structure of populations of the Red Kangaroo *M. (O.) rufus* because only 8 months of drought is sufficient to kill all the juveniles in a population; and much longer droughts have been known in central Australia. Further evidence that drought can cause age structures such as that seen at Spring Creek is given in Shipman (1975).

The massive, poorly-sorted black clay overlying the bone layer is also concordant with the drought hypothesis. Shipman (1975) notes that such deposits are often found overlying drought-affected fossil faunas and are formed when rain removes soil from the surrounding areas which have been denuded by drought and overgrazing.

Drought undoubtedly affects some species more severely than others. Main (1978) suggests that large forms are at a disadvantage in water stress situations. Some evidence suggests that this was the case at Spring Creek. Table 9 shows that there are no juveniles of the large herbivores but there are of the smaller forms. The lack of small animals in general in the deposit may indicate that they were not as severely affected by the drought as were the large forms. Only larger samples of bones from the site will show if this interpretation is correct.

Our hypothesis for the origin of the bone accumulation is as follows. A drier and colder climate existed at Spring Creek than occurs there at present. Drought conditions had persisted in the area for several years. Most of the juveniles of the large mammal species had died and no new young had been successfully reared. The season of death for most of the adults might well have been summer because of the increased water stress and because of the *Pimelea* seeding time (late summer). The animals may have been drawn to water from widely separate localities and the surviving adults that gathered around an open stretch of water in the sluggishly flowing creek may have eaten out the surrounding vegetation. When the animals died over a short period of time, their carcasses provided a food resource for

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Thylacoleo carnifex. When the winter rains came, they may have been heavy enough to choke the creek with a considerable depth of sediment derived from the denuded surrounds which had been severely affected by drought and overgrazing.

CONCLUSIONS

1. A diverse megafaunal assemblage survived in southwestern Victoria until at least 20,000 ybp.
2. The Spring Creek bone accumulation is probably the result of a population that was catastrophically killed and buried soon after decomposition of the carcasses. Drought is the most likely cause of death and most readily explains the age structure of animals from the site.
3. The co-existence of species which today live in widely separate habitats is probably the result of the colder and drier climatic conditions prevalent at the time.

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The following Museum of Victoria Department of Vertebrate Palaeontology registration numbers refer to the specimens in the Spring Creek collection. Mostly dental fragments only are registered: *Macropus giganteus titan* P157249-P157287, P157387, P157384, P157386, P157385. *Macropus (Osphranter) rufus* P157288, P159935. *Macropus agilis siva* P157302-157306, P157388. *Protemnodon* cf. *anak* P157293. *Protemnodon* sp. cf.

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P. brehus P42526. *Sthenurus andersoni* P159934, P159295. *Simosthenurus gilli* P157394, P157396, P157397. *Simosthenurus occidentalis* P157301 *Thylacoleo carnifex* P157307, P157319. *Palorchestes azeal* P157320, P157309. cf. *Sarcophilus* P157311: *Diprotodon* sp. P157312. *Zygomaturus trilobus* P157313-157317, P157389. small macropodine P159945. cf. *Tribonyx mortierii* P159947. Murid, P157318.

Relative Efficiency of Two Pitfall-drift Fence Systems for Sampling Small Vertebrates

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ABSTRACT

The efficiencies of two pitfall-drift fence systems, one incorporating two traps and able to capture from two principal directions, the other using one trap and able to sample mainly from one direction, were compared in a variety of habitats in monsoonal Northern Australia. Based on trap-night effort (where one pitfall operated for one night equals one trap-night), the two systems were equally efficient in most habitats, and proved particularly useful for sampling ground-dwelling reptiles and amphibia. However differences between the two systems were apparent through the capture of large numbers of amphibia in partially inundated habitats. This effect seems to be due mainly to differing orientations of drift fences relative to the water's edge, rather than to differences in the directional sampling capabilities or size of opening between the two designs.

For survey work the double-pit system is recommended, as it records a much larger number of species in a set time, but it should be used in conjunction with conventional trapping and detection methods for comprehensive results.

INTRODUCTION

Although pitfall traps have been utilized for a considerable time in ecological work overseas (e.g. Banta 1957; Andrzejewski and Wroclawek 1963), they have only in the last decade gained wide acceptance in Australia. They have proven useful in small vertebrate survey work (Mather 1979, Hopper 1981, Menkhurst 1982) and in the study of some insect communities (Greenslade and Greenslade 1971, Watt 1980). Pitfall traps appear to be particularly effective in the more arid habitats (Cockburn *et al.* 1979) and have facilitated the discovery or extension of range of several small species (Aitken 1977, Fleming and Cockburn 1979, Kitchener 1980).

However the design and methodology of pitfall trap systems have been largely a matter of personal choice, the selection of materials influenced by cost

and local availability. Most methodological studies of pitfall trapping have compared them to snap traps or live traps (e.g. Chelkowska 1967, Pelikan *et al.* 1977, Boonstra and Krebs 1978, Cockburn *et al.* 1979), although Luff (1975) investigated the features influencing the efficiency of several types of pitfall traps. In Australia, only the study of Braithwaite (1983) has compared different pitfall trap systems in the field; viz. single pits with drift fences or with lids ajar.

This study compares two pitfall-drift fence systems which were operated simultaneously in a variety of habitats during a survey of small vertebrates in the monsoonal region of the Northern Territory.

MATERIALS AND METHODS

Trapping was conducted on 35 sites along the forested ecotone between the South Alligator River floodplains and the higher woodlands on CSIRO's Kapalga study area, 160 km east of Darwin in the Northern Territory. The climate is monsoonal, with 80% of the mean annual rainfall (1536 mm) falling during the humid wet season between December and March (data for Darwin, Commonwealth of Australia 1981). Temperatures are generally high throughout the year, ranging between a mean maximum of 33.8°C in November and a mean minimum of 19.6°C in July (data for Darwin, Commonwealth of Australia 1981).

The 35 sites were apportioned in a stratified random design to six habitats on the basis of their areas calculated from colour aerial photographs. These habitats represent a gradient in elevation and duration of inundation viz:

- (i) "Wet" paperbark, a gallery forest dominated by *Melaleuca* spp. and flooded for most of the year;
- (ii) "Dry" paperbark, as above, but flooded for only 4-5 months;
- (iii) Lawn, a low grassland dominated by short grasses and sedges with scattered *Pandanus spiralis* and temporarily inundated in the wet season;
- (iv) White gum, a low woodland with *Eucalyptus alba* and *E. papuana* the main overstorey species, often with an understorey of *Cassia obtusifolia* or *Hyptis suaveolens*, and flooded only for short periods after heavy rain;
- (v) Monsoon forest, a closed forest non-eucalypt community occurring only in small pockets with some lower-lying areas temporarily inundated; and
- (vi) Appletree, a low woodland dominated by *Syzygium suborbiculare* with an understorey mainly of *Cassia obtusifolia*, occurring in small patches on higher ground.

Sampling was conducted in the mid-wet (December-February) and mid-dry seasons (June-August) on each site in 1981 and 1982. The two pitfall systems used were:

(a) Single pit, consisting of P.V.C. drainpipe (15 cm diameter and 40 cm deep with an earthen floor) with a fibreglass insect screen drift fence (7 m long, 30 cm high) supported by five equally-spaced wooden stakes. The fence was erected in a shallow V, with the pitfall at the inside centre of the angle, just touching the fence. This system could therefore sample only from one principal direction.

(b) Double pit, consisting of two metal ice-cream drums (23 cm diameter and 30 cm deep with a perforated floor to allow drainage) placed approximately 6.5 m apart, with

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a 7 m drift fence (as for single pits) erected straight between them on their diameter axes. This system could sample from two principal directions.

The two systems were placed 5-10 m apart at each site and in the 1981 wet season were operated for seven consecutive nights. Thereafter, due to logistic considerations, traps were operated for four consecutive nights and were checked and cleared at least once a day. Orientation of drift fences was generally arbitrary, but in some cases was determined by the density of vegetation or condition of the soil surface. Records were kept of drift fence orientation on all sites and trapping sessions.

RESULTS

A total of 871 individuals comprising 28 species (1 mammal, 12 reptile and 15 amphibian species) were captured in 1480 trap-nights (where one pitfall operated for one night equals one trap-night), with 255 individuals being recorded in the single pit system and 616 in the double pit system. Based on effort (i.e. trap-nights) significantly more individuals were captured in the double pits than

in the single ($\chi^2_1 = 5.0, 0.1 < p < 0.05$), but this result was habitat and seasonally specific (see later). Eighteen species were recorded in the single pits and 26 in the double, with two species being captured exclusively in the single pits and ten species only in the double pits (see Tables 1 and 2).

WET SEASON

Twenty-two species and 313 individuals were recorded in 691 trap-nights during the two wet seasons, with 1.5 times as many species and 2.2 times as many individuals being recorded in the double pit system (Table 1). However, based on number of individuals and trap-nights (i.e. trap success or relative efficiency) there was no significant difference between the two systems

($\chi^2_1 = 0.2, 0.5 < p < 0.7$). For both systems, trap successes were generally

highest in the temporarily inundated habitats (e.g. lawn) and lowest in wet paperbark where traps were frequently rendered non-functional by flooding during the trapping periods. Significant differences between the two pitfall systems were apparent in white gum, where more individuals (mainly of *Cyclorana australis* and *Limnodynastes convexiusculus*) were captured in the single pits, and in the lawn habitat, where more individuals (mainly of *C. australis* and *Ranidella bilingua*) were captured in the double pits (Table 1). These differences are explained by differential orientation of drift fences between the two pitfall systems at some sites (see Discussion).

Captures of amphibia outnumbered those of reptiles by a factor of 8.6 in the single pit system and 4.4 in the double pit system. In general, for both trap types the discrepancy between reptile and amphibian captures was greatest in those habitats that were temporarily inundated (e.g. lawn and dry paperbark)

TABLE 1. Relative efficiencies and numbers of species and individuals recorded by single (S) and double (D) pitfall systems — wet season.

SPECIES	HABITATS and TRAP-NIGHTS																TOTALS	
	Wet paperbark				Dry paperbark				Lawn		White gum		Monsoon forest		Appletree			
	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D
11	22	22	22	44	43	86	85	180	40	92	22	44	223	468				
MAMMALS: <i>Planigale maculata</i>																		
REPTILES: <i>Heteronotia binoei</i>																		
<i>Diporiphora bilineata</i>																		
<i>Lophognathus temporalis</i>																		
<i>Varanus timorensis</i>																		
<i>Carlia foliorum</i>																		
1				1		3	4	15		1		1	3	2				
<i>Carlia gracilis</i>																		
<i>Cryptoblepharus plagiocephalus</i>																		
<i>Ctenotus essingtonii</i>																		
<i>Sphenomorphus crassicaudus</i>																		
<i>Sphenomorphus douglasi</i>																		
<i>Stegonotus cucullatus</i>																		
AMPHIBIA: <i>Litoria dahlii</i>																		
<i>Litoria rubella</i>																		
1										1								
<i>Litoria nasuta</i>																		
<i>Litoria latopalmata</i>																		
<i>Litoria tornieri</i>																		
<i>Cyclorana australis</i>																		
<i>Cyclorana longipes</i>																		
<i>Platyplectron ornatus</i>																		
<i>Limnodynastes convexisculus</i>																		
<i>Ranidella bilingua</i>																		
NUMBER OF SPECIES																		
1	2	3	7	7	7	8	8	15	3	8	6	8	13	20				
NUMBERS OF INDIVIDUALS																		
1	2	4	19	25	92	50	69	6	18	11	17	97	216					
Chi-square tests (for individuals)																		
NA																		
$\chi^2 = 2.0^{NS}$																		
$\chi^2 = 7.5^{**}$																		
$\chi^2 = 5.4^*$																		
$\chi^2 = 3.3^{NS}$																		
$\chi^2 = 0.5^{NS}$																		
$\chi^2 = 0.2^{NS}$																		
Relative efficiency (trap success)																		
0.09	0.09	0.18	0.43	0.58	1.07	0.59	0.38	0.15	0.19	0.50	0.38	0.43	0.46					

NA sample size too small; NS non-significant; * $p < 0.05$; ** $p < 0.01$

EFFICIENCY OF TWO PITFALL SYSTEMS

TABLE 2. Relative efficiencies and numbers of species and individuals recorded by single (S) and double (D) pitfall systems — dry season.

SPECIES	HABITATS and TRAP-NIGHTS																TOTALS	
	Wet paperbark			Dry paperbark			Lawn		White gum		Monsoon forest			Appletree				
	S	D	S	S	D	S	D	S	D	S	D	S	D	S	D	S	D	
30	60	31	62	61	122	85	170	40	80	16	32	263	526					
MAMMALS: <i>Planigale maculata</i>																		
REPTILES: <i>Heteronotia binoei</i>																		
<i>Carlia foliorum</i>						1	2									1	2	
<i>Carlia gracilis</i>			9	19	1	4	10	2									3	
<i>Cryptoblepharus plagiocephalus</i>																	32	
<i>Ctenotus essingtonii</i>						14	10										1	
<i>Sphenomorphus crassicaudus</i>					1	1	2	1						1	5	15	15	
<i>Sphenomorphus douglasi</i>					3	1	4							1	3	3	3	
<i>Ramphophyllaps torelli</i>							1										6	
AMPHIBIA: <i>Litoria dahlii</i>																		
<i>Litoria bicolor</i>	1	1		1												1	2	
<i>Litoria rubella</i>	11	2	1	2		1										12	5	
<i>Litoria rothi</i>				1													1	
<i>Litoria nasuta</i>			1				1	1									1	
<i>Litoria tornieri</i>	1						1	1									2	
<i>Litoria microbelos</i>																	2	
<i>Platyplectron ornatus</i>																	1	
<i>Limnodynastes convexiusculus</i>	9	29	12	54	14	12	9	11	7				28			51	134	
<i>Ranidella bilingua</i>	10	20	35	127	5	25	1	3	1				5			52	180	
<i>Uperoleia inundata</i>						1		3					1				5	
<i>Uperoleia lithomoda</i>								2									2	
NUMBER OF SPECIES																		
NUMBERS OF INDIVIDUALS																		
Chi-square tests (for individuals)																		
Relative efficiency (trap success)																		
1.06	0.92	1.87	3.30	0.38	0.38	0.40	0.30	0.25	0.46	0.06	0.18	0.60	0.76					
NA sample size too small; NS non-significant; * p<0.05; *** p<0.001																		

NA sample size too small; NS non-significant; * $p < 0.05$; *** $p < 0.001$

and least in the drier habitats (e.g. appletree). The single mammalian species *Planigale maculata* accounted for only 8.3% of captures (Table 1).

DRY SEASON

Overall, results were similar to those from the wet season. Twenty-one species and 558 individuals were recorded in 789 trap-nights, with 1.7 times as many species and 2.5 times as many individuals being recorded in the double pit

system (Table 2). Significantly more individuals ($\chi^2_1 = 6.3, 0.01 < p$

< 0.05) were recorded in the double pits, but this difference was due entirely to large numbers of *L. convexiusculus* and *R. bilingua* being captured in the double pits on several of the dry paperbark sites (Table 2). In all other habitats trap successes were not significantly different between the two systems. For both trap types relative efficiency was greatest in the lower elevation habitats (e.g. paperbarks) where some water was still present, and lowest in the driest habitat, appletree.

These trends are due mainly to captures of amphibians, which outnumbered those of reptiles by factors of 3.2 and 5.4 for single and double pit systems respectively. In both trap systems captures of reptiles outnumbered those of amphibia only in the two driest habitats, white-gum and appletree. For each type of trap the proportional representation of species from the two herpetofaunal groups changed between the habitats, consistent with the gradient in elevation and degree of aridity. Such a trend is not unexpected, given the differing physiological adaptations of reptiles and amphibians (Cogger 1979), and is supported by other results from this survey (Friend, unpublished data). As in the wet season, *Planigale maculata* was the only mammal species recorded, accounting for only 0.5% of captures (Table 2).

COMPARISONS OF SPECIES DETECTION RATES

To further compare the relative abilities of the two pitfall systems for detecting species in vertebrate surveys, the cumulative number of species recorded was plotted against both time (measured as days of trapping) and effort (measured as trap-nights) for the two systems. This was done separately for the two wet and two dry seasons involved.

All functions were of similar form, there being an initial linear increase ($r = 0.88$ or greater, $p < 0.001$) in the (cumulative) number of species recorded with time or effort, followed by a "plateau" as no (or very few) further species were recorded. Typical examples of these functions are shown in Figures 1 and 2 for the 1981 dry season. Statistical tests (Student's *t* test; Zar (1974), p228-9) were carried out to ascertain whether the slopes (β) of the linear portions of these curves differed between the two pitfall systems (Table 3).

EFFICIENCY OF TWO PITFALL SYSTEMS

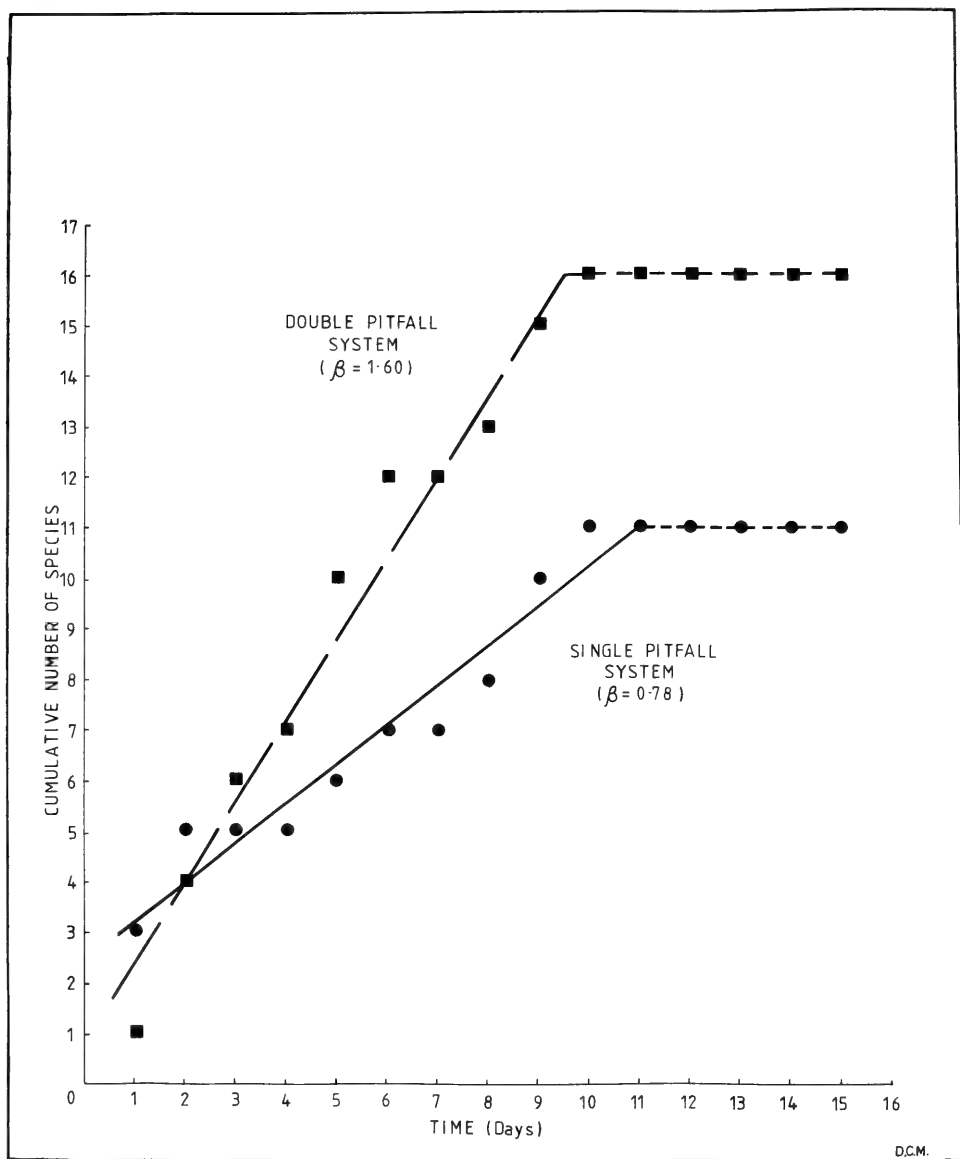


Fig. 1. Species — time functions for single (●) and double (■) pitfall-drift fence systems — dry season 1981.

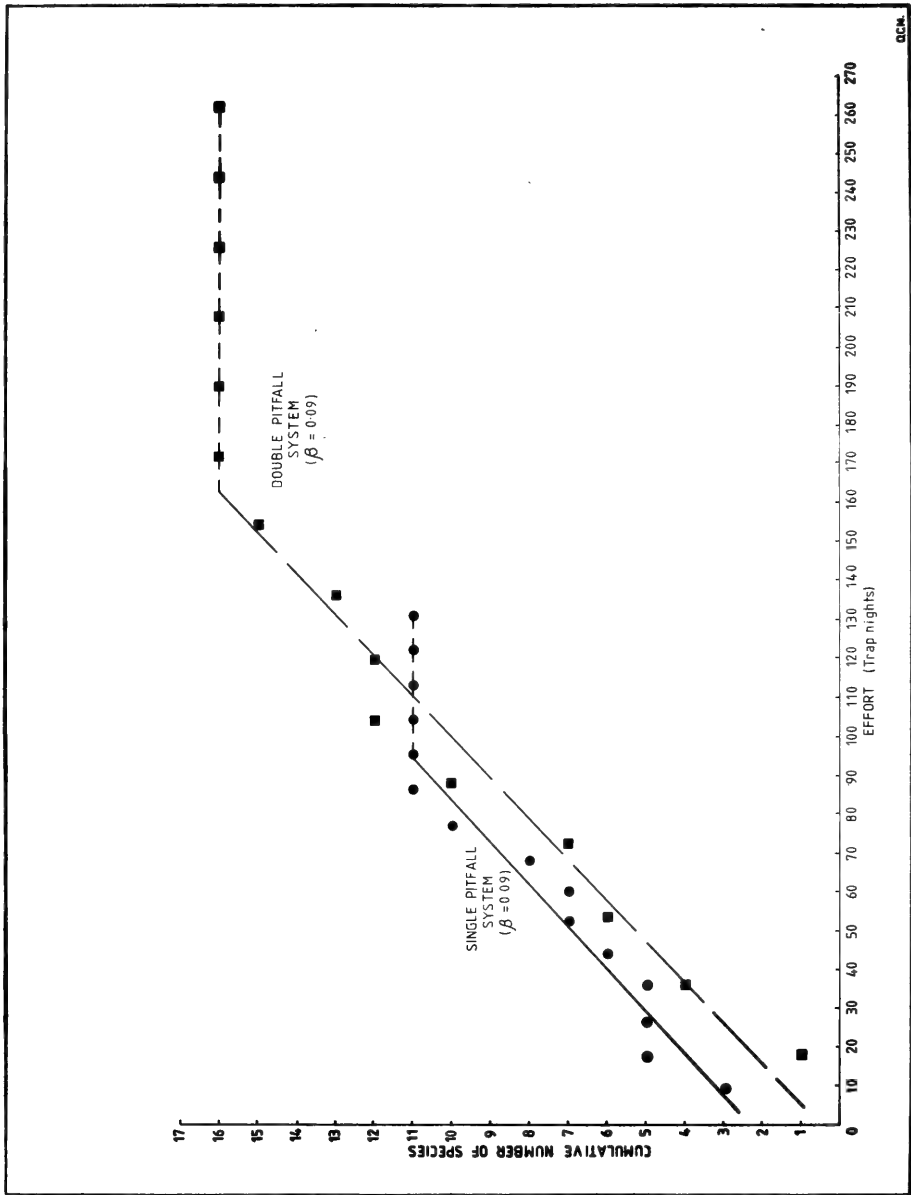


Fig. 2. Species — effort functions for single (●) and double (■) pitfall-drift fence systems — dry season 1981.

EFFICIENCY OF TWO PITFALL SYSTEMS

TABLE 3. Comparisons of linear regression coefficients (slope, β) of species/time (S/T) and species/effort (S/E) functions for single (S) and double (D) pitfall systems.

1981								1982							
Wet season				Dry season				Wet season				Dry season			
S/T		S/E		S/T		S/E		S/T		S/E		S/T		S/E	
S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D
0.43	1.15	0.06	0.07	0.78	1.60	0.09	0.09	1.03	1.07	0.13	0.06	0.35	0.82	0.04	0.05
t = 9.2***		t = 1.4 ^{NS}		t = 6.4***		t = 0.2 ^{NS}		t = 1.6 ^{NS}		t = 5.1***		t = 5.9***		t = 0.4 ^{NS}	

NS non-significant; *** $p < 0.001$

In all cases except the wet season of 1982, the slope of the species/time curve was significantly greater for the double pitfall system ($p < 0.001$), but the slopes of the species/effort curves did not differ significantly between the two systems ($p > 0.1$, Table 3). In the 1982 wet season, however, the slopes of the species/time curves were not significantly different ($0.1 < p < 0.2$) for the two pitfall systems, but the single pitfall system's species/effort function had significantly greater slope than that of the double pitfall system ($p < 0.001$, Table 3).

DISCUSSION

Based on number of individuals and trap-nights, there was no significant difference between the two pitfall-drift fence systems in most habitats. This is in spite of the fact that (a) the double pit system can capture from both sides of the fence and therefore should theoretically catch twice as many individuals per trap-night as the single pit system; and (b) the double pitfalls were 135% larger in the area of their openings than the single pitfalls. The differences that were apparent between the two systems were always attributable to differential capture efficiency of amphibia, which in turn appeared to be greatly dependent on the orientation of the drift fences relative to the edge of standing water. Observations suggest that large numbers of ground-dwelling frogs were caught at sites close to water when drift fences were parallel with the water's edge, thus intercepting frogs as they moved between the water and higher ground (see also Gibbons and Bennet 1974). Differential orientation of drift fences seemed to be a more important factor than both the two-directional sampling capabilities and the larger openings of the double pit system in explaining differences in efficiency between the two designs. However it is likely that size of opening could become an important factor if diameter differences were further increased, but this could only be verified by keeping all other variables constant (e.g. number of traps, depth of traps, orientation and length of drift fences).

When species detection rates for the two systems are compared, results indicate that the double pitfall system generally is able to detect more species and at a significantly faster rate in time than the single pitfall system. However on a species per trap-night (effort) basis the two systems are quite similar. Although such results are not unexpected, they do show that for the purposes of small vertebrate survey work, the double pit system is superior. The differing results for the 1982 wet season may be due to the extremely wet conditions which were experienced during trapping. The single pitfalls may be relatively more efficient at retaining individuals when partial inundation occurs, because their earthen floors allow water to escape, whereas the holes in the metal floors become blocked with mud.

Both systems proved quite effective for sampling reptiles and amphibians, and were able to show trends in the relative importance of these two groups across a moisture gradient, which are supported by other evidence (Friend, unpublished data). However these pitfalls were ineffective in catching the large small mammals such as *Rattus colletti*, which was a relatively common species on these sites in the two wet seasons, based on captures in conventional cages and metal traps (Friend, unpublished data). It is most likely that this and similar-sized species are able to escape from pitfalls of the type used here. Hopper (1981) also commented on the problems of using pitfall traps for surveying small mammal communities, although they may be more efficient than conventional traps for certain species or age-classes of animals (Boonstra and Krebs 1978, Cockburn *et al.* 1979).

Although some physical effort is required to install pitfall-drift fence systems for large vertebrate surveys, this should not present a problem (except in particularly hard substrate), given the availability of portable post-hole diggers (Braithwaite 1983). Furthermore, for surveying heterogeneous areas, pitfall systems with relatively short drift fences are considerably more versatile and easier to install than the multi-pitfall type frequently used with fences 50-100 m in length (see also Braithwaite 1983).

The double pit system could probably be further improved by use of baits if certain species or types of animals were sought (Boonstra and Krebs 1978, Greenslade and Greenslade 1971, Watt 1980), by slightly lengthening the drift fence, and by using different materials for the pitfalls (e.g. glass, Luff 1975) or providing a sheltering system over the trap (Braithwaite 1983). In particular, considerably deeper pitfalls (e.g. two of the drums stacked one on the other with the upper drum's end removed) could prevent the potential escape of the larger saltatorial species (e.g. *Litoria nasuta*). Such modifications are dictated by the aims of a particular study, and could be tested prior to its commencement.

Clearly though, for survey work (Banta 1975, Pelikan *et al.* 1977, Cockburn *et al.* 1979, Hopper 1981) or even for single species population studies (Boonstra and Krebs 1978) pitfall traps should be used in conjunction with conventional trapping and other detection methods if comprehensive results are to be achieved.

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A Method of Using Gastroliths to Calculate Length and Weight of the Freshwater Crayfish, *Cherax destructor*, for Use in Predatory-prey Studies

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ABSTRACT

A method is described for calculating the carapace length (CL, in mm) of the freshwater crayfish, *C. destructor*, from gastrolith disc length (GDL, in mm), independent of moult stage. $CL = 7.07GDL + 1.78$.

A length-weight relationship is given, to allow the weight (W, in g) of the crayfish to be calculated. $W = 5.015 \times 10^{-4} CL^{3.027}$.

The method should be applicable to other gastrolith-forming decapod crustaceans. Gastroliths are often found in the stomachs of fishes and water-birds, in cormorant nests and in aboriginal middens; this method will be useful in dietary studies of such predator-prey relationships.

INTRODUCTION

The freshwater crayfish, *Cherax destructor* Clark, commonly known as the yabby, is distributed over a large part of the Australian mainland (Riek 1969), being found in most freshwater bodies within the Lake Eyre and Murray-Darling basins. It is an important prey species for many aquatic vertebrates.

C. destructor forms a significant part of the diet of many inland fishes, including the Murray cod and the callop (or golden perch). It is preyed upon by introduced fishes such as brown and rainbow trout (Faragher 1980), carp (*Cyprinus carpio*, personal observation) and redfin (Hale 1925), and by many water-birds including white ibis (Carrick 1969) and cormorants (McNally 1957; Miller 1979). Regurgitated gastroliths are commonly found in cormorant nests (L.C. Llewellyn, personal communication). The yabby is significant in the diet of the eastern water rat (Woollard *et al.* 1978), and it is likely that it is eaten by the platypus, also. Man, too, has been an important predator of the yabby, and anthropologists (at Australian National University, Canberra, and Victoria Archaeological Survey, Melbourne) have found yabby remains, in particular the

gastroliths, in aboriginal middens (K. Kefous and M. Smith, and P. J. F. Coutts, personal communications). Other decapods which are similarly preyed upon include the New Zealand freshwater crayfish, *Paranephrops zealandicus*, whose gastroliths have been found in perch, trout and shag stomachs (Scott and Duncan 1967).

The gastroliths are a pair of hard rounded bodies which occur in some species of decapod crustaceans. They are located on the sides of the cardiac stomach, and make their first appearance in the early stages of the moult cycle (Travis 1960); they continue to grow to their maximum size, at which time moult occurs. The gastroliths are then cast off, together with the cuticular lining of the crayfish's stomach, wherein they come to lie. There they are dissolved, and their calcium store resorbed.

During and for some time after moulting, the yabby, like all crustaceans, is most vulnerable to predation. Because the gastroliths are composed mainly of calcium salts, and are the least digestible part of the crayfish, they may remain in a predator's stomach for a considerable time. As the size of crayfish eaten is often of interest to researchers studying the feeding habits of a predator, I set out to find a way of determining the size of the crayfish from the size of its gastrolith.

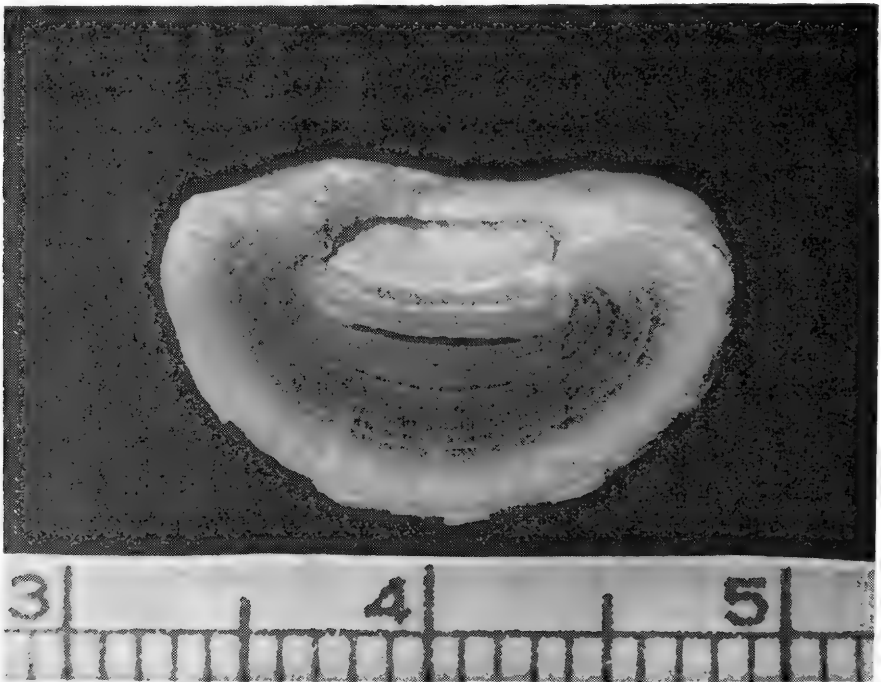


Fig. 1a. A fully developed gastrolith, split along the long axis, showing the disc and the layered structure of the gastrolith. Scale unit is 1 cm.

CALCULATING CRAYFISH SIZE FROM GASTROLITHS

It is important to note that neither weight nor overall length of the gastrolith are suitable parameters, as both these vary with the moult state of the animal. However, situated in the anterior lateral walls of the cardiac stomach is a pair of oval vascular areas, the gastrolith fields, by which the gastroliths are formed during the premoult period. The first layer laid down by each field on the cuticular lining of the stomach is the gastrolith disc (Travis 1960). The gastrolith field thus provides the pattern for the gastrolith disc. As more layers are added, and the convexity of the gastrolith increases, the field necessarily enlarges and distorts to accommodate the growing gastrolith. The thin layers (or lamellae) of the gastrolith can be readily seen in cross-section (Fig. 1a).

MATERIALS AND METHODS

The crayfish examined in this study were collected from farm dams near Narrandera in New South Wales during 1975 and 1976. Preliminary examination indicated that the length of the gastrolith disc would be correlated with animal size. It is the long axis of this oval disc which is measured to obtain the gastrolith disc length (GDL) (Fig. 1b).

Gastrolith disc length was measured to the nearest 0.1 mm using a low-power microscope fitted with an ocular micrometer. Carapace length (CL), measured from the

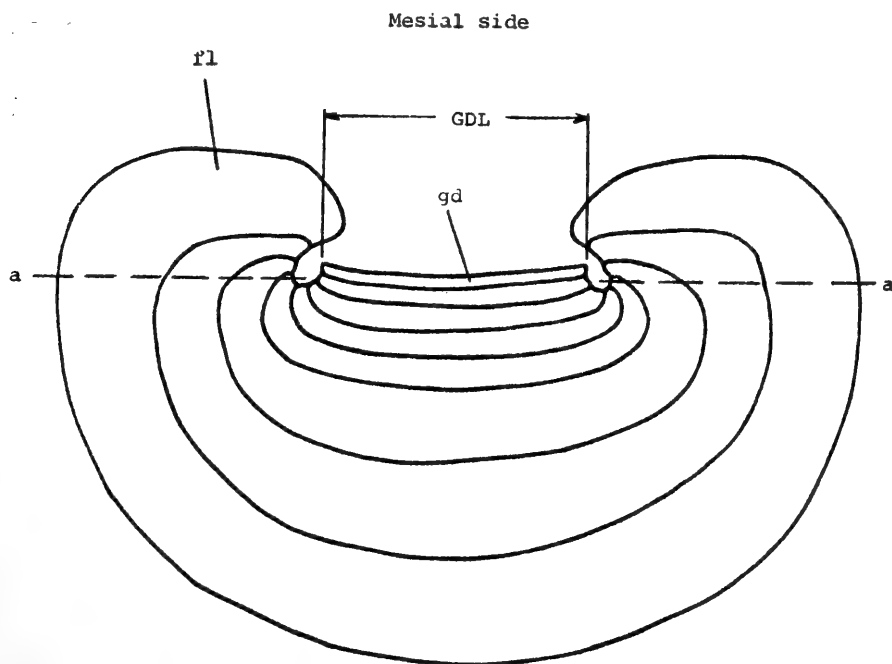


Fig. 1b. Diagram of a fully developed gastrolith, sectioned along the long axis, showing the method of measuring gastrolith disc length (GDL), and the way in which the final layers recurve over the plate. Line a—a indicates the approximate location of the mesial surface of the eroded gastrolith shown in Fig. 3.
fl, final layers; gd, gastrolith disc; GDL, gastrolith disc length.

posterior edge of the orbit to the posterior edge of the carapace, parallel to the midline, was used as the measurement of body size. CL was recorded to the nearest millimetre below the observed value, the centre-point of each 1 mm interval being used in the calculations. Values of CL less than 10 mm (used in deriving the length-weight relationship) were measured to the nearest 0.1 mm. The data were subjected to regression analysis, CL being regressed on GDL.

In determining the CL-GDL relationship, gastroliths from crayfish in various stages of moult (see Travis 1960) were examined. GDL was easily measured in early premoult gastroliths but, as a gastrolith reaches its full development, the final layers often recurve over and partially obscure the disc (Fig. 2). In order to measure GDL in these cases it was necessary to split the gastrolith by placing a sharp knife or scalpel on the mesial surface (the flat or concave surface) of the gastrolith and pushing down forcibly.

In a small percentage of gastroliths the disc was found to be bent sharply. These were considered anomalous and ignored in the calculation of the relationship.

Postmoult gastroliths were not used in calculating the relationship, since the accuracy in measuring their GDLs is not as high as for premoult gastroliths, because of the effects of erosion (but see Discussion section). This erosion is due to digestion and abrasion in the crayfish's stomach (Fig. 3).

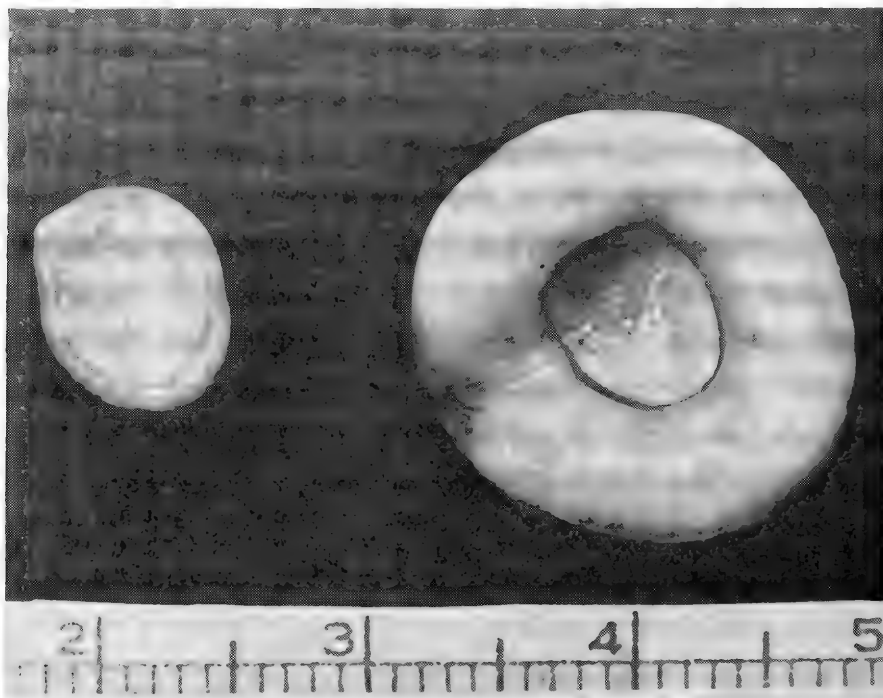


Fig. 2. Gastroliths of *C. destructor*, showing the disc on the mesial surface. The gastrolith on the left is from crayfish in early premoult; that on the right is fully developed and is from an animal about to moult. Note that the disc of the latter is partially obscured by the recurving of the outer layers. Both discs are actually about the same size. Scale unit is 1 cm.

CALCULATING CRAYFISH SIZE FROM GASTROLITHS

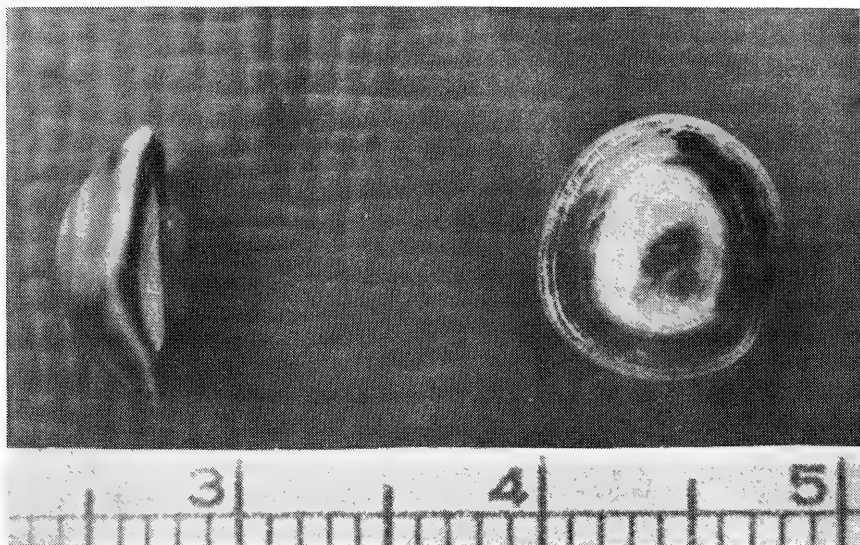


Fig. 3. Postmoult gastroliths, removed from the stomach of a crayfish. Note the erosion, particularly of the mesial (flattened) surfaces. (See also Fig. 1b.) Scale unit is 1 cm.

Total weight (W) of each crayfish was measured in grams, to an accuracy of $\pm 5\%$, after a standard drying which consisted of rolling the animal in absorbent cotton towelling for a few seconds. Moulting and postmoult animals were not measured, nor were egg-bearing females and those with missing or regrown appendages. The data were subjected to regression analysis, W being regressed on CL .

RESULTS

CARAPACE LENGTH — GASTROLITH DISC LENGTH RELATIONSHIP

A sample of 70 crayfish, of approximately equal numbers of each sex, was examined, with CL ranging from 13.5 to 61.5 mm. GDL ranged from 1.6 to 9.1 mm. Separate regressions of data were performed for each sex and analysis of covariance showed no significant difference between the regressions ($P > 0.05$). The data were combined and are plotted in Fig. 4. Regression analysis of these data gave the linear relationship:

$$CL = 7.07GDL + 1.78 \quad (r = 0.98)$$

where CL and GDL are in mm, r = correlation coefficient.

LENGTH-WEIGHT RELATIONSHIP

A sample of 86 crayfish, of approximately equal numbers of each sex, was examined, with total weights ranging from 0.016 to 245 g. CL ranged from 2.8 to 73.5 mm. Separate regressions of data were performed for each sex and analysis of covariance showed no significant difference between the regressions ($P > 0.05$).

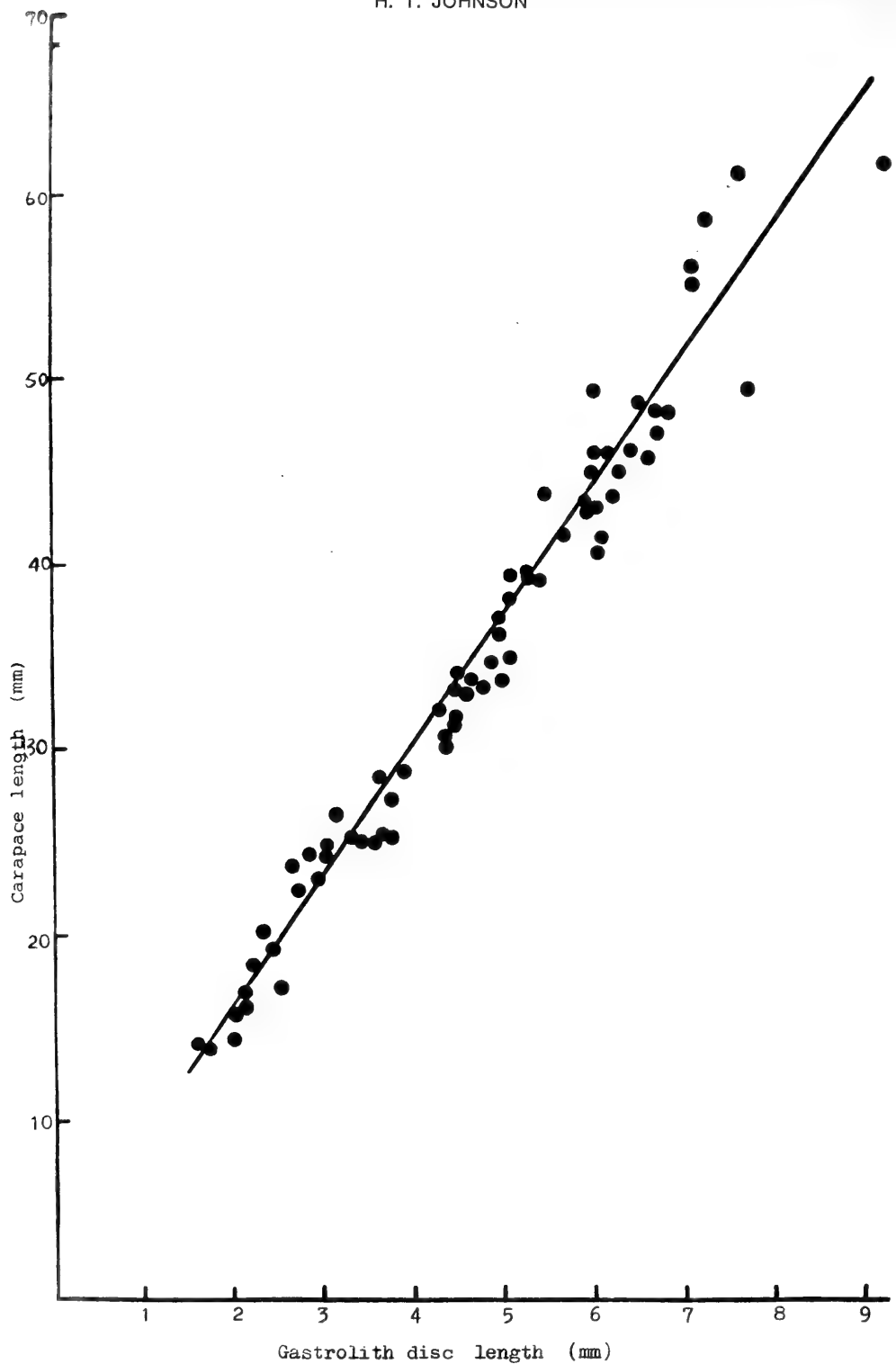


Fig. 4. Relationship between carapace length and gastrolith disc length in *C. destructor*.
 $CL = 7.07GDL + 1.78$, $r = 0.98$, $n = 70$.

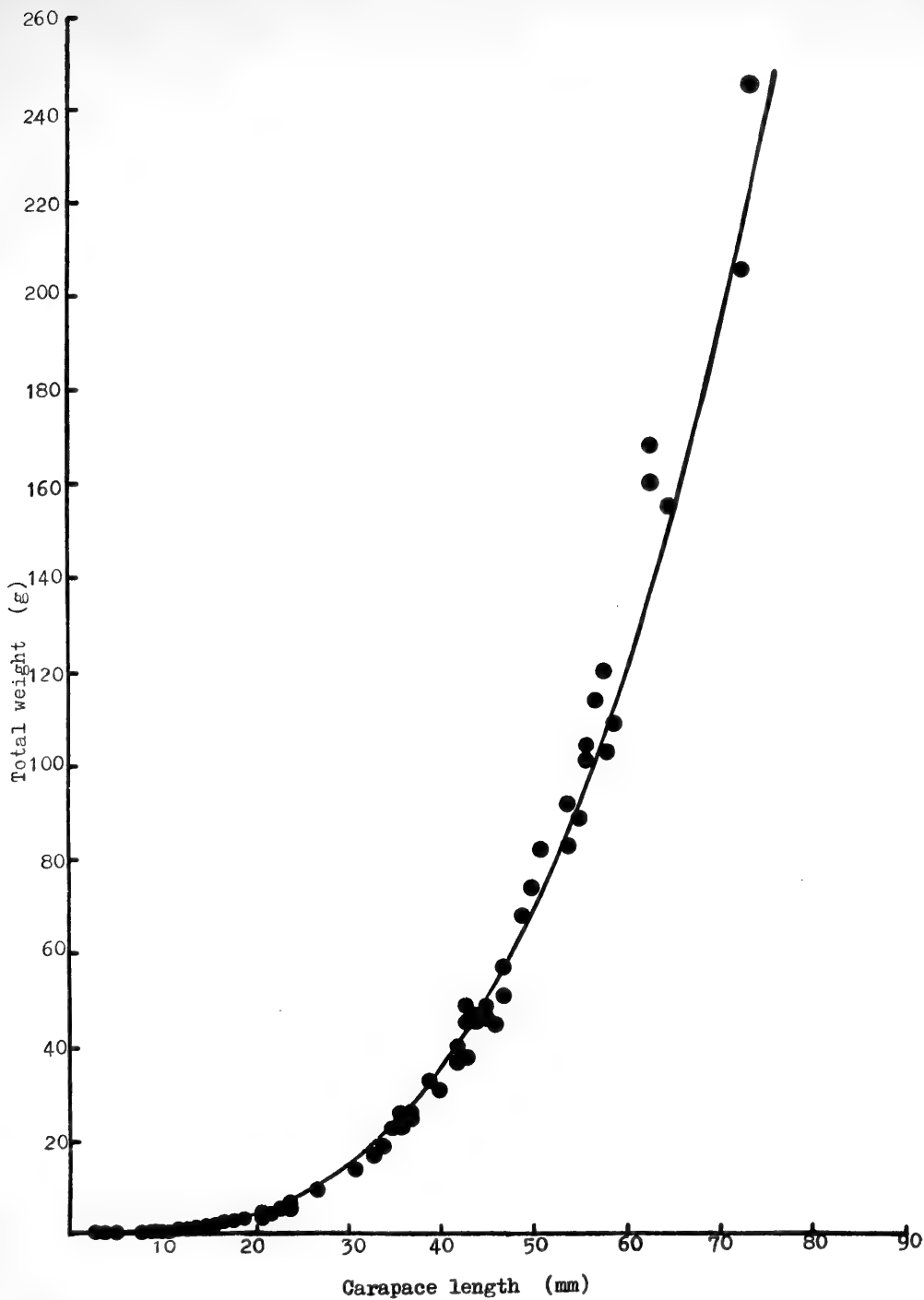


Fig. 5. Relationship between total weight and carapace length in *C. destructor*.
 $W = 5.015 \times 10^{-4} CL^{3.027}$, $r = 0.99$, $n = 86$.

The data were combined and are plotted in Fig. 5. Regression analysis of these data gave the relationship: $W = 5.015 \times 10^{-4} CL^{3.027}$ ($r = 0.99$) where W is in grams and CL in mm, r = correlation coefficient.

DISCUSSION

The relationship between CL and GDL provides an accurate method of calculating the CL of the crayfish eaten. Similarly, the relationship between W and CL provides an accurate method of calculating the weight of the crayfish from the CL .

Gastroliths are found in many decapod crustaceans, notably the freshwater crayfishes, several marine Reptantia (e.g. the lobster, *Homarus*), and certain land crabs (Passano 1960), and it seems likely that this method could be applied to other gastrolith-forming decapods. Identification of the decapod species may be possible using morphological characteristics of the gastrolith. If not, the crustacean may be identifiable, knowing its distribution, the area in which the predator was captured, and the predator's feeding habits.

An extension of the method allows calculation of the quantity of edible flesh, for use in dietary or bioenergetics studies. Reynolds (1980) determined the edible flesh yield of *C. destructor* to be 19-27%, and also found the edible flesh to consist of 88.6% protein.

Gastroliths are sometimes found in an eroded state, either because they are postmoult gastroliths which have become eroded in the crayfish's stomach (see Materials and Methods section, and Fig. 3), or because they have been partially digested in a predator's stomach, which often causes the outer layers to flake off in patches. However, in both these cases, the disc is not affected until a good part of the gastrolith has been eroded, especially in fully developed gastroliths. Even severe abrasion (e.g. the gastrolith in Fig. 3) still allows the disc margin to be fairly well discerned as the innermost ring on the flat of the gastrolith. Thus, in most eroded gastroliths, GDL can be measured reasonably accurately.

It is worth noting that gastroliths from very small crayfish are not commonly found in predators' stomachs. It is likely that, because of their size, small gastroliths are digested relatively quickly. Also, Scott and Duncan (1967) have suggested that small crayfish, having softer exoskeletons than larger animals, are more attractive to predators, and are therefore eaten at all stages of the moult cycle. Thus, the chance of observing small gastroliths in a predator's stomach would be lower than that of larger gastroliths.

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The Macro-benthic Fauna of Brackish Water Prawn Farming Ponds at Port Stephens, New South Wales

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ABSTRACT

Core samples, collected regularly from two tidal 0.11 ha earthen prawn farming ponds, contained only 17 species of macro-benthic fauna, although additional macro-benthic species were collected from the ponds by other methods. Most of the macro-benthic animals in the core samples were polychaetes (98.3% of all individuals and 82.3% of biomass on an ash-free dry weight basis). The polychaetes *Prionospio cirrifera*, *Barantolla lepte* and *Notomastus torquatus* which all belong to the subclass Sedentaria were particularly common. One of the two ponds contained a high level of macro-benthic biomass but little detritus while the second pond was the reverse. This latter pond supported higher prawn growth and survival rates in synchronous prawn farming trials with greasyback prawns (*Metapenaeus bennettiae*). The stomach contents of the prawns from these two ponds contained much more detritus than macro-benthos.

INTRODUCTION

Earthen prawn farming ponds usually contain greater pelagic and macro-benthic faunal populations than more artificial prawn habitats (aquaria or intensive culture units, e.g., raceways). However except for the recent study by Rubright *et al.* (1981), little is known about this macro-benthic fauna especially in terms of their importance as food items for prawns (Maguire 1980). The purpose of the present study was to describe the pond macro-benthos and where possible to relate these fauna to pond management and production of greasyback prawns (*Metapenaeus bennettiae*). This paper complements a study of the fish fauna of these ponds by Maguire and Bell (1982).

MATERIALS AND METHODS

SAMPLING METHODS AND SITES

Sediment core samples were taken in two 0.11 ha ponds at the Brackish Water Fish Culture Research Station, Port Stephens, N.S.W. Maguire and Bell (1982) described

these square ponds and the tidal range for this location. A reference area within a subtidal *Halophila* seagrass bed (mostly *H. ovalis*) in the Port Stephens estuary was also sampled and has been described by Gibbs *et al.* (1984). This is the only genus of seagrass which colonises the ponds (mostly *H. decipiens*) although it was not present during the period when core samples were collected from the two ponds.

Within a pond or reference station, 13 sediment cores (20 cm diameter, 10 cm deep) were collected with a stainless steel, diver operated corer. Pond cores were taken at 5 m intervals along the two non-diagonal axes bisecting each pond. These transect lines extended across the pond floor but not up the sloping walls. A random sampling pattern was used for collecting each set of 13 cores from the reference station. After core samples were collected they were washed through a 1mm mesh sieve and preserved in 10% (v/v) formalin. Macro-fauna were subsequently sorted from the residual vegetation, detritus and shell grit prior to identification and enumeration. The core sampling dates are shown in Table 1. With two exceptions, the ponds and reference station were sampled (a) prior to the pre-stocking application of rotenone, an ichthyocide, (b) after the stocking of postlarval prawns, (c) at two months and (d) four months after stocking, and (e) at six months after the prawns were harvested. The two samples not collected were the first sample for the reference station (because of contamination with oyster lease debris) and the last sample in pond B (in use for another study).

Additional macro-benthic fauna were collected on other occasions, from these and two other 0.11 ha ponds at the Research Station, when they were observed on pond bottoms or walls or in prawn sampling and harvesting nets or in occasional sediment cores.

POND MANAGEMENT

As details of the farming methods and results will be provided in a subsequent paper only a brief summary is given here. The two ponds were poisoned with rotenone to kill all fish and were subsequently refilled after a week of tidal water exchange with each pond raceway and drainage valve open (see Maguire and Bell 1982). Each pond was stocked with approximately 50,000 hatchery reared, postlarval greasyback prawns (approx. 5 mm total length). A pelleted, artificial diet designed for trout (Rural Chemicals Pty. Ltd., Glenorie, N.S.W.) was usually provided at a rate of 2.5-5.0% of estimated biomass per day. The ponds were regularly fertilised and continuously aerated (see Maguire *et al.* 1981). For at least six months prior to the application of rotenone in ponds A and B and for six months after harvesting in pond A, normal tidal water exchange occurred; i.e. it was usually only restricted by the permanent 2 mm mesh screens at the

TABLE 1. Timetable for macro-benthos sampling and pond management during synchronous greasyback prawn farming trials (A, B = ponds A, B, E = estuarine reference station).

Sampling Site	Dates	Number of weeks	Event
A, B	15-16/12/75	0	1st macro-benthos samples taken.
A, B	22/12/75	1	Ponds poisoned with rotenone to kill all fish.
A, B	30/12/75	2	Each pond stocked with 50,000 postlarval prawns.
A, B, E	6/1/76	3	2nd macro-benthos samples taken.
A, B, E	4/3/76	11	3rd macro-benthos samples taken.
A, B, E	28/4/76	19	4th macro-benthos samples taken.
A, B	5-16/8/76	33-35	Prawns harvested.
A, E	27/1/77	58	5th macro-benthos samples taken.

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TABLE 2. Particle size distribution in sediment samples from two ponds (A, B) and an estuarine reference station E ($\bar{x} \pm \text{S.E.}$).

Sediment fraction *	Particle size (μm)	Percentage size distribution		
		A	B	E
Mud	<63	24.7 \pm 5.8 ^a	5.8 \pm 0.5 ^b	17.4 \pm 2.1 ^a
Very fine sand	63-125	5.0 \pm 1.6 ^a	0.3 \pm 0.1 ^b	0.7 \pm 0.1 ^b
Fine sand	125-250	20.1 \pm 1.7 ^a	10.1 \pm 0.5 ^b	19.0 \pm 4.0 ^a
Medium sand	250-500	45.4 \pm 7.8 ^a	77.8 \pm 0.5 ^b	57.7 \pm 5.1 ^a
Coarse sand	500-1000	4.4 \pm 0.6 ^a	6.0 \pm 0.3 ^a	5.2 \pm 0.4 ^a
	>1000	0.4 \pm 0.2 ^{**}	— **	— **
Organic content (g/kg dry wt.)		88.5 \pm 23.7 ^a	12.2 \pm 1.5 ^b	22.5 \pm 1.2 ^b

ab Within each row values sharing a common superscript are not significantly different ($P>0.05$) according to the Least Significant Difference analyses; * According to Folk (1968); ** No comparisons made.

end of the raceways leading to the ponds (Maguire and Bell 1982). However, in between stocking and harvesting, additional 300 μm plankton mesh screens were inserted in the raceways of both ponds.

A detailed summary of pond salinity and temperature readings for the duration of this study is given in Maguire and Bell (1982). The ranges for monthly averages of pond minimum and maximum water temperatures and pond salinity were 10.5-23.5°C, 14.5-28.0°C and 22.0-30.0 ppt. in that order during the farming trials. Occasional dissolved oxygen measurements were made during the present study using the Winkler method for samples collected near the pond bottoms during mid-morning.

SEDIMENT PARTICLE SIZE AND ORGANIC CONTENT ANALYSES

After the last macro-benthos sampling date (Table 1), five sediment samples were collected in each pond and the reference station using the same 20 cm diameter corer. The particle size distribution (Table 2) within 200 g subsamples was then determined using the standard methods of Folk (1968).

Macro-benthic animals and plants were removed from 2 cm deep sediment cores (five per pond) and the organic content determined by ashing the dried sediment in a muffle furnace for 6 hr at 600°C. The biomass (ash free dry weight) of macro-benthic animals was determined by using the same ashing method on approximately 95% of the total number of individuals collected. The remainder were weighed and retained for reference collection purposes. Their biomass values were estimated using wet weight to ash free dry weight conversion values determined for various taxa when most of the individuals were ashed.

PRAWN STOMACH CONTENT ANALYSES

Approximately 50 prawns per pond were preserved in 20% (v/v) formalin. The stomach (proventriculus) of each prawn was dissected out and the contents examined with a binocular microscope. The relative percentages of the various dietary components were determined by the points (estimated volumetric) method (Pollard 1973). The stomach fullness of each prawn was estimated using a 0-5 (empty-very full) ranking system. No

trout food was added to the ponds for two days prior to the sampling of prawns for stomach content analysis. This was to overcome the problem of distinguishing between pond bottom detritus and digested pellets. Inadvertent pooling of the prawn samples from the two ponds prevented dietary comparisons being made between the two prawn populations.

NUMERICAL ANALYSES

Sampling efficiency was assessed by using a computer program to calculate a smoothed and averaged species-area curve for each sampling location and time. The average number of species was calculated for all possible combinations (C) of choosing the x th sample from a total of n samples without replacement.

$$C_x^n = \frac{n!}{x!(n-x)!} \quad \text{where } 0! = 1$$

The analytical techniques used for comparing different sites and sampling times were essentially those of multivariate classification and ordination. Classification clusters individuals into related groups by comparing dissimilarity measures calculated between all individuals with respect to all attributes. The C.S.I.R.O. computer program MULCLAS (Lance and Williams 1967 a,b), an agglomerative polythetic analysis, calculated a dissimilarity measure between individuals (core samples) using the abundance of each attribute (macro-benthic species) in each core sample. It was used with the Canberra metric dissimilarity measure

$$D_{ij} = \sum_{k=1}^s \frac{|X_{ik} - X_{jk}|}{X_{ik} + X_{jk}}$$

where D_{ij} is the dissimilarity measure between the i -th and j -th samples, s is the number of species and X_{ik} is the number of individuals of species k in sample i (Williams 1976). The analysis successively fuses the individuals to form a hierarchy which can be represented in a dendrogram.

The data were then ordinated using principal co-ordinate analysis to elucidate the inter-group relationships thus determining whether the samples form a continuum arbitrarily divided by classification or whether samples are clustered in relatively homogenous groups clearly separated from each other (Goodall 1973). The ordination was performed using the C.S.I.R.O. computer program GOWER. An associated diagnostic program GOWECOR calculated the correlation coefficients of the species associated with the principal axes (eigenvectors) which explained a substantial proportion of the variance (Lance *et al.* 1968, Williams 1976).

RESULTS AND DISCUSSION

STATISTICAL ANALYSES

The overall differences in sediment particle size distribution among sampling sites were examined by performing a one way analysis of variance for each major sediment fraction. Individual comparisons between ponds or between a pond and the estuarine reference station for each sediment fraction were made using least significant difference techniques (Steel and Torrie 1960).

SAMPLING EFFICIENCY

For each sampling location and time the species-area curve showed that the number of species recorded in 10 cores was at least 80% of the number for 13 cores. The 80% level is a somewhat arbitrary measure of sampling efficiency

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TABLE 3. Benthic fauna collected in 117 sediment cores from two prawn farming ponds. (Mean and maximum abundance values are based on single core results expressed on a per m² basis. The minimum abundance value was zero for all species.)

Organism	No. of individuals per m ² (Abundance)			
	Pond A		Pond B	
	mean	maximum	mean	maximum
Crustacea				
<i>Acetes australis</i>	—		10.4	(572.4)
<i>Callianassa arenosa</i> *	—		9.2	(63.6)
<i>Victoriopisa australiensis</i>	1.5	(63.6)	—	
Mollusca (Bivalvia)				
<i>Ennuncula</i> sp. *	—		0.6	(31.8)
<i>Notospisula trigonella</i> *	—		0.6	(31.8)
<i>Wallucina assimilis</i>	—		0.6	(31.8)
Mollusca (Gastropoda)				
<i>Nassarius burchardi</i> *	1.5	(95.4)	—	
Polychaeta				
<i>Armandia intermedia</i>	6.4	(159.0)	—	
<i>Barantolla lepte</i> *	5.9	(63.6)	607.0	(2416.8)
<i>Capitella</i> sp. *	1.0	(31.8)	22.0	(159.0)
<i>Heteromastus filiformis</i> *	1.0	(31.8)	37.3	(318.0)
<i>Leonnatus stephensoni</i> *	—		1.2	(63.6)
<i>Magelona</i> sp. *	1.5	(31.8)	6.7	(31.8)
<i>Mediomastus californiensis</i> *	0.5	(31.8)	1.2	(31.8)
<i>Nephtys australiensis</i> *	6.8	(159.0)	5.5	(95.4)
<i>Notomastus torquatus</i> *	7.8	(95.4)	46.5	(286.2)
<i>Prionospio cirrifera</i>	61.2	(1017.6)	550.7	(6487.2)

* Also recorded from the reference station.

but it does suggest that the sampling program was adequate for characterising which macro-benthic species were present on each occasion provided that they could be readily enclosed by the corer.

DESCRIPTION OF MACRO-BENTHIC FAUNA

The species which were present in the core samples from ponds A and B are listed in Table 3. Polychaetes, most of which were from the subclass Sedentaria, accounted for 98.3% of all individual macro-benthic animals obtained from these pond cores and 82.3% of their biomass on an ash-free dry weight basis. *Prionospio cirrifera*, *Barantolla lepte* and *Notomastus torquatus* were particularly common. Rubright *et al.* (1981) found that polychaetes from subclass Sedentaria were also very abundant in sediment from prawn farming ponds in Texas (U.S.A.). The two Port Stephens ponds were generally similar in terms of the species composition of their macro-benthic fauna. However, pond B cores often contained *Callianassa arenosa* ("yabbies" or "nippers") and up to 200 similar burrows, some definitely inhabited by *C. arenosa*, could be found in an individual 1 m²

TABLE 4. Additional macro-benthic fauna recorded from four prawn farming ponds.

Organism	Organism
Asciadiacea <i>Microcosmus</i> sp. ^b <i>Styela plicata</i> ^b	Mollusca (Bivalvia) <i>Anadara trapezia</i> (Sydney cockle) <i>Saccostrea commercialis</i> (Sydney rock oyster) ^b <i>Laternula creccina</i> (lantern shell) ^a <i>Sanguinolaria donacioides</i> (sunset shell) <i>Tellina deltoidalis</i> ^a <i>Xenostrobus securis</i> (mussel) ^b
Bryozoa <i>Bugula neritina</i> ^b <i>Conopeum tenuissimum</i> ^b	Mollusca (Gastropoda) <i>Aplysia</i> sp. (sea hare) ^a <i>Bembicium auratum</i> ^b <i>Dolabella auricularia</i> (sea hare) <i>Pyrazus ebeninus</i> (whelk) <i>Salinator fragilis</i> <i>Velacumantus australis</i> (whelk)
Crustacea <i>Balanus variegatus cirratus</i> (barnacle) ^b <i>Calliopius</i> sp. (amphipod) <i>Cymadusa</i> sp. A (amphipod) <i>Cymadusa</i> sp. B (amphipod) <i>Heteropanope serratifrons</i> (crab) <i>Lucifer</i> sp. (luciferid shrimp) <i>Macrobrachium intermedium</i> (carid shrimp) <i>Metapenaeus macleayi</i> (school prawn) <i>Metapenaeus bennettiae</i> (greasyback prawn) <i>Nerocila</i> sp. (isopod) <i>Palaemon serenus</i> (carid shrimp) <i>Paragrapsus laevis</i> (crab) <i>Penaeus plebejus</i> (eastern king prawn) <i>Sesarma erythrodactyla</i> (crab)	Nemertinea Nemertean Polychaeta <i>Ceratonereis</i> spp. <i>Galeolaria</i> sp. ^b <i>Marphysa sanguinea</i> ^a <i>Phyllodoce</i> sp. ^a <i>Sabella</i> sp. Scyphozoa <i>Cassiopea</i> sp.

a Also recorded from the reference station; b Usually only found on hard surfaces within the pond.

quadrat is pond B. It is likely that the shallow corer used in the ponds was an inefficient sampling device for this deep-burrowing species. *C. arenosa* was not found in pond A.

The macro-benthic fauna found in the pond cores included only 17 species although an additional 37 species (Table 4) were collected from all four ponds on other occasions by hand or from cores or sampling and harvesting nets. Several of these additional macro-benthic species only grew on hard surfaces and thus were not widely distributed across the pond bottoms. Some species only occurred occasionally although they could be numerous when present; e.g. the jellyfish *Cassiopea* sp. has at times densely covered a pond bottom (up to 30 jellyfish in an individual 1 m² quadrat) while in its inverted, benthic feeding position. In addition, there are several species listed in Table 4 which were often observed in the ponds but not in the core samples from ponds A and B. These species include the shrimp *Palaemon serenus*, the crab *Paragrapsus laevis* and three species of penaeid prawns *Metapenaeus macleayi*, *M. bennettiae* and *Penaeus plebejus*. This last species is the most abundant naturally-recruited, penaeid prawn in the ponds. The bivalves *Laternula creccina*, *Sanguinolaria donacioides* and *Tellina*

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deltoidalis have occurred periodically in the ponds at high densities, e.g., up to 380 *L. creccina* in a 3.3 m² area (115 per m²). The whelk *Pyrazus ebeninus* is normally common in the ponds although usually on the submerged sections of the pond walls.

Gibbs *et al.* (1984) have described the species composition of the macro-benthic fauna in the reference station but a summary is provided in Table 5. There were some similarities between the fauna of the ponds and the reference station with 71% of the macro-benthic species found in the pond core samples also being recorded from the reference station samples. Furthermore, the two groups of core samples were dominated by polychaetes both in terms of numbers of species and individuals.

TABLE 5. Relative abundance of organisms from major taxonomic groups in sediment cores from two ponds and an estuarine reference station in Port Stephens, N.S.W.

Taxon	No. of species (% of total No.)		No. of individuals per m ² (% of total No.)	
	Ponds A, B*	Ref. stn. E	Ponds A, B*	Ref. stn. E
Crustacea	3 (17.6%)	11 (17.2%)	21.1 (1.5%)	13.9 (2.4%)
Mollusca Bivalvia	3 (17.6%)	7 (10.9%)	1.8 (0.1%)	6.0 (1.0%)
Gastropoda	1 (5.9%)	12 (18.8%)	1.5 (0.1%)	14.8 (2.5%)
Polychaeta	10 (58.8%)	26 (40.6%)	1278.1 (98.3%)	511.0 (87.1%)
Others	0 (0%)	8 (12.5%)	0 (0%)	40.7 (7.0%)
TOTAL	17	64	1302.5	586.4

* The results for all the cores from the regular sampling programme in both ponds have been pooled.

SPECIES RICHNESS OF POND MACRO-BENTHIC FAUNA

Maguire and Bell (1982) found that the fish fauna of these four Port Stephens ponds was relatively diverse. In contrast, the core sample data in Table 5 indicates that the macro-benthic fauna in ponds A and B, in comparison with that of the reference station, was relatively species deficient. The presence of a large number of additional macro-benthic species in the four ponds (Table 4) does not necessarily detract from this latter conclusion. Many of the species listed in Table 4 were not easily sampled with the corer because they were fouling organisms on vertical walls or were relatively large and mobile animals or occurred only intermittently. An equivalent supplementary list of macro-benthic fauna could reasonably be expected to result from occasional sampling with a variety of collecting devices over several years at the reference station.

Several factors could have directly caused the macro-benthos of ponds A and B to be relatively species-deficient. The 64 macro-benthic species recorded from the nearby reference station could be considered as potential colonizers of the ponds yet only 17 of these species were recorded from any of the four ponds

either in core samples or otherwise (Tables 3, 4). Larval or postlarval stages of these species would have had to move from the Port Stephens estuary into the 200 m long, tidal, artificial canal leading to ponds and then through screens (2 mm or 300 μ m and 2 mm) in the raceways between the canal and the ponds. Colonization of the ponds by larval or postlarval stages of some macro-benthic fauna may have been more inhibited by these obstacles than colonization by larval or postlarval fish with better developed swimming behaviour.

Another factor which could be suggested as a reason for the low species richness of macro-benthos in the ponds was the presence of fish in the ponds both prior to the first core samples and later during the farming trials themselves. The poisoning of the ponds prior to the stocking of postlarval prawns indicated that fish (mostly juvenile sea mullet *Mugil cephalus*) were abundant in pond B but not pond A. During the farming trials fish (again mostly juvenile sea mullet) only became common in pond A. Thus their presence could not explain the low species richness in both ponds throughout the study. Furthermore, the detritivorous feeding habits of juvenile sea mullet (Maguire and Bell 1981, S.P.C.C. 1981a) are likely to have little direct impact on macro-benthic fauna.

NUMERICAL ANALYSES

In addition to providing information on the relative species richness of the three sites, the core sample results were analysed with numerical methods which took account of changes through time in the abundance of individual macro-benthic animals. The classification arranged the samples into three major groups corresponding to the reference station and the two prawn farming ponds with the two ponds being more similar to one another than to the reference station. No subgroups which indicated time trends were apparent. The ordination (Fig. 1) clearly demonstrated the homogeneity of the pond samples (A and B) and the heterogeneity of the reference station samples (E). Eigenvector 1, which accounted for 34.0% of the variance within the data and separated the farming ponds from the reference station, appears to relate to the presence or absence of seagrass at the sampling sites. Eigenvector 3, which separated the two prawn ponds and accounted for 14.2% of the variance may be related to sediment differences. Pond A had a finer sediment with greater organic content (much of it as coarse leaf and detrital material) than pond B (Table 2).

The differences in the macro-benthos at the three sampling stations are exemplified in Fig. 2. It should be noted that although the number of individuals and the biomass values for cores have been expressed on a per m² basis, this extrapolation would not be valid for the number of species. Analysis of the number of species (S), the abundance (N) and biomass (BM) shows that pond A was characterised by a small but relatively stable macro-benthic community while pond B, although still characterised by a small number of species, underwent an increase in both faunal density and biomass. The reference station (E) was usually more species rich and temporally more variable than the ponds. There was,

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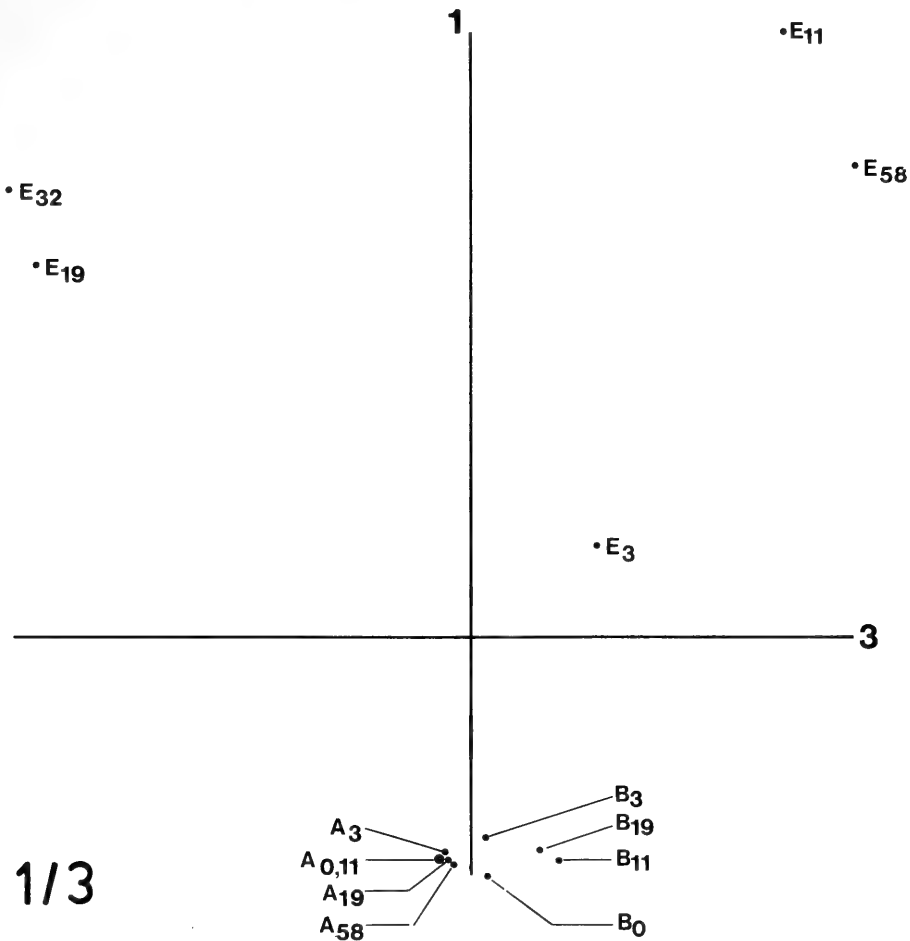


Fig. 1. Ordination results (vector 1 on vector 3) for core samples taken in two prawn farming ponds (A, B) and an estuarine reference station (E) during weeks 0-58.

however, some similarity between pond B and the reference station in terms of changes in abundance and biomass through time.

In the case of pond A it is possible that the relatively uniform size of the coarse leaf litter and detritus on the surface of this pond bottom caused the food diversity of the sediment to be low and hence unsuitable for a rich invertebrate fauna (Whitlatch 1981). In contrast, the macro-benthos in pond B increased in density despite the relatively high density of stocked greasyback prawns. Other species of prawns appear to adversely affect the densities of a wide variety of

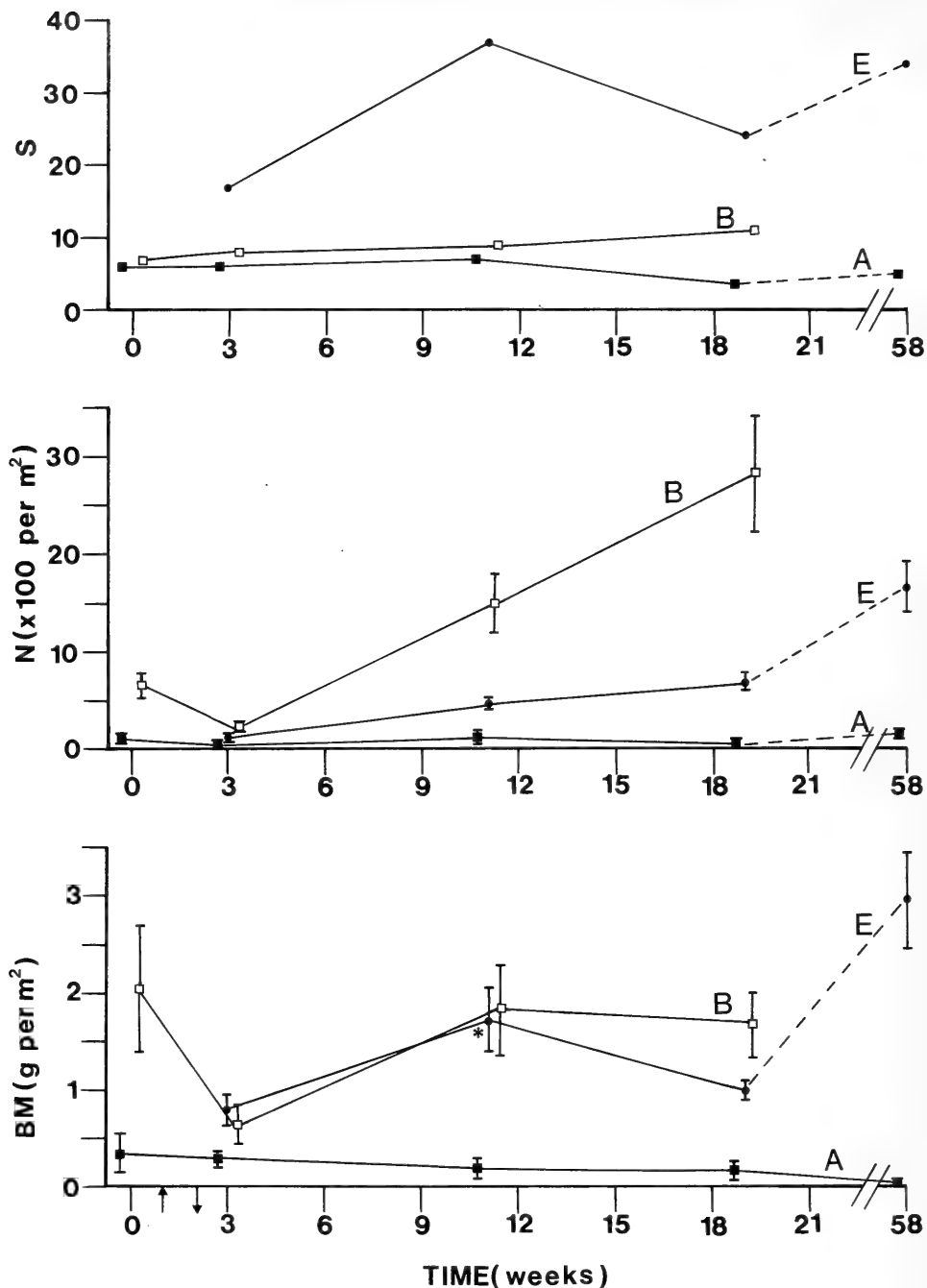


Fig. 2. The changes in the numbers of species (S) and individuals (N) and biomass (BM as grams ash-free dry weight per m²) throughout the sampling period in two ponds (A, B) and an estuarine reference station (E). The arrows indicate the dates on which both ponds were treated with rotenone and stocked respectively. The symbol * indicates that the E11 week biomass value excludes the biomass of a relatively large specimen of the crab *Dromidia* sp. Including this crab makes the E11 value 3.35 g/m² \pm 1.66 ($\infty \pm$ S.E.).

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TABLE 6. Stomach (proventriculus) contents of greasyback prawns^a collected from two prawn farming ponds.

Parameter	Result
No. of stomachs examined	99
No. of empty stomachs	35
Fullness index ^b	1.4
Dietary item (%) ^c	
Detritus	82.8
Crustaceans	11.3
Polychaetes	3.9 ^d
Nematodes	1.4
Sand	0.3
Diatoms	0.3

a Size range 14-25 mm carapace length (C.L.); b Mean value based on a subjective 0 (empty) to 5 (very full) ranking system; c % of volume of stomach contents (mean of values recorded for each individual); d Predominantly composed of segments and setae of the errant polychaete *Ceratonereis* spp.

macro-benthic fauna (Nelson 1981). In the present study (Table 6) and in those by Dall (1968) and Moriarty (1976), the contribution of macro-benthic fauna to the diets of greasyback prawns was relatively small and thus this species of prawn may have less effect on the density of macro-benthic organisms than some other penaeid species.

The reference station was included in the sampling program to see if any major changes in the pond macro-benthos corresponded with similar changes in the Port Stephens estuary. However, the greater temporal variation among the reference station samples limited their usefulness for this purpose. The increased species richness and temporal variation at station E may be related to the presence of a vegetated substrate (*Halophila ovalis*). The presence of vegetation has been shown to be a principal determinant in separating both macro-benthic (Powis and Robinson 1980) and fish faunal communities (S.P.C.C. 1981b). It is also apparent that reduced species richness occurs in muddy unvegetated habitats (Gray 1974, Hutchings et al. 1978) and it is thought that this is due to the reduced physical complexity of the habitat (Kohn and Leviten 1976, Heck and Wetstone 1977). Thus it is likely that the pond macro-benthos would change when *Halophila* is abundant within the ponds for extended periods.

EFFECT OF ROTENONE ON POND MACRO-BENTHOS

Monitoring of the macro-benthos during the two prawn farming trials provided some information on the effects of rotenone, the ichthyocide used in the ponds prior to stocking. The week 0 and week 3 results allow a comparison of the macro-benthos before and after poisoning of the ponds. This comparison reveals that in both ponds a substantial component of the macro-benthos survived the application of rotenone. Thus there was little change in the number of species present in each pond (Fig. 2) and the ordination analysis (Fig. 1) did not indicate

TABLE 7. Growth and survival results for greasyback prawns (*M. bennettiae*) from two 0.11 ha prawn farming ponds^a.

Parameter	Pond A	Pond B
Stocking density (post larvae/m ²)	45.4	45.4
Average prawn wt. ($\bar{x} \pm \text{S.E.}$) at harvest (g)		
male	3.03 \pm 0.05	2.74 \pm 0.08
female	3.64 \pm 0.09	2.92 \pm 0.13
Percentage recaptured	18.4	9.7
Estimated survival rate (%) ^b	19.8	11.6
Estimated biomass at harvest (g/m ²) ^b	30.0	14.7

a The duration of the farming trials was 32 weeks; b Based on both the number of prawns actually harvested and the number estimated to have remained in the pond.

a large change in the macro-benthos between week 0 and week 3 in either pond. However, there were significant declines in the total numbers of individuals (N) in both ponds ($P < 0.05$, t-test). There was also a decline in the biomass value in each pond but only the pond B result was significant ($P < 0.01$). These declines were largely due to reductions in the densities of the polychaetes *Barantolla lepte* and *Prionospio cirrifer*.

PRAWN PRODUCTION AND STOMACH CONTENTS

The results of the two prawn farming trials (Table 7) were not promising in terms of prawn production but were interesting with respect to the relative amounts of macro-benthos and detritus in the two ponds. Prawn growth and survival results were clearly better in pond A than in pond B. These ponds exhibited little consistent difference in pond bottom dissolved oxygen levels ($\bar{X} \pm \text{S.E.}$ for ponds A and B were 7.2 ± 1.1 and 6.3 ± 1.4 mg/l respectively). The ponds clearly differed in terms of sediment coarseness but this is unlikely to account for the difference in prawn production results for the two ponds (see Aziz and Greenwood 1982). A more likely reason is the greater amount of detrital food in pond A as indicated by the sediment organic results (Table 2). Similarly, Edwards (1977) attributed the faster growth rate of *Penaeus vannamei* at one estuarine site to the higher organic content of the sediment at this site. The gut content results (Table 6) also suggest that a pond with a high detrital content but little macro-benthos would contain a greater amount of natural food for greasyback prawns than would a pond with little detritus but abundant macro-benthos. The contribution of natural food to the diet of prawns within ponds can be significant (Maguire 1980, Maguire and Bell 1981).

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Distribution of Mallophaga on the Australian Magpie (*Gymnorhina tibicen* Latham) (Family: Cracticidae)

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ABSTRACT

Ischnocera were collected from live magpies (*Gymnorhina tibicen*). *Philopterus* and *Bruelia* were found on all host-types (mainland white-backed, black-backed, western and Tasmanian magpies); *Philopterus* was less common than *Bruelia*. A significantly lower proportion of white-backed magpies than black-backed magpies were infested with *Bruelia*. Seasonal changes in the percentage of birds infested with *Bruelia* and *Philopterus* were observed, with highest numbers of parasites in autumn and winter and the lowest numbers in summer.

INTRODUCTION

The Australian magpie (*Gymnorhina tibicen* Latham) shows considerable variation in plumage colour throughout its range. Initially magpies were collected for taxonomic analysis, but an effort was made to collect sufficient Mallophaga on the different plumage types so as to compare their densities and distributions.

There are three distinct forms in the species *G. tibicen*. The black-backed form inhabits most of northern and central Australia, a white-backed form is found in south-eastern Australia and Tasmania and a western form (where males are white-backed and females are black-backed) is found in south western Australia (Slater 1974). There is very little difference between the three mainland forms, when comparing biochemical or morphological characters (Hughes 1980). However, the magpies from Tasmania are quite distinct from mainland magpies, when compared using multivariate morphometric analysis (Hughes 1980).

Three genera of Mallophaga occur on the magpie. They are *Philopterus* and *Bruelia*, which belong to the Division Ischnocera, family Philopteridae; and *Myrsidea*, which belongs to the Division Amblycera, family Menoponidae. There is only a single species of *Bruelia*, *B. semiannulata* Piaget. The mainland magpies are infested with a single undescribed species of *Philopterus* and the Tasmanian magpies may be hosts for a second species (Hughes 1980). Neither type has been described, and specimens have been sent to R.L.C. Pilgrim (University of Canter-

bury, N.Z.), who is currently working on their taxonomy. Mallophaga live amongst the feathers of their host and feed on feathers and/or blood (Clay 1958). Some inhabit specific parts of the body of the host (e.g. *Philopterus* which lives on head and neck feathers) whereas others roam all over the host (e.g. most Amblycerans).

Little work has been carried out on their ecology. Ash (1960) examined a large number of live passerine birds (belonging to five species) and studied seasonal changes in louse density, numbers of different louse species per host and their distribution on the host. He found large variations in all these factors, with different Mallophagan and host species. Other workers have been involved mostly with examining dead specimens (e.g. Foster 1969) or with domestic birds (Nelson 1971, Crutchfield and Hixon 1943).

The purpose of this study was firstly to determine whether or not *Bruelia* and *Philopterus* occurred in equal densities on the various host-types and secondly to determine whether there were differences in the incidence of louse infestation between host types. Because some previous work suggested seasonal changes in lice density (Ash 1960) and increases in population size correlated with host breeding times (Foster 1969), the data were examined for seasonal variation, since this may affect conclusions about density variation with host-types.

MATERIALS AND METHODS

COLLECTION OF LICE

A total of 276 magpies were examined for lice between 1974 and 1979. These birds were trapped, using a live magpie as a decoy. Areas from which birds were sampled are shown in figure 1. Due to difficulties with sample sizes, all magpies collected within a 200km radius of certain localities were included (Fig. 1). Magpies were divided into five categories, based on back colour and geographic locality. Tasmanian magpies were separated from mainland birds because they are distinct in biochemical and morphometric characters (Hughes 1980). The four categories selected were white-backed, black-backed, western and Tasmanian.

Each bird was examined systematically working down the back, from the head to the insertion of the tail, examining each feather and collecting lice of all stages. The process was then repeated on the underside of the bird. This procedure ensured that a similar proportion of the total number of lice present was collected from each bird. Because *Philopterus* occurs on head and neck feathers, which are smaller and easier to search, it is probable that a greater proportion of the population of this species was collected than of *Bruelia*, which is more common on the back feathers, which are more difficult to search. If no lice were found after this procedure had been carried out, the bird was said to be 'clean'.

The number of lice observed on live birds is only a part of the total number present. However, it is assumed that this number is proportional to the actual number present and that the data from live birds can therefore be used to make comparisons between different host-types. Also, most analysis involved comparisons between individual birds which had lice and those which did not, so that the actual number present was ignored.

MALLOPHAGA ON THE AUSTRALIAN MAGPIE

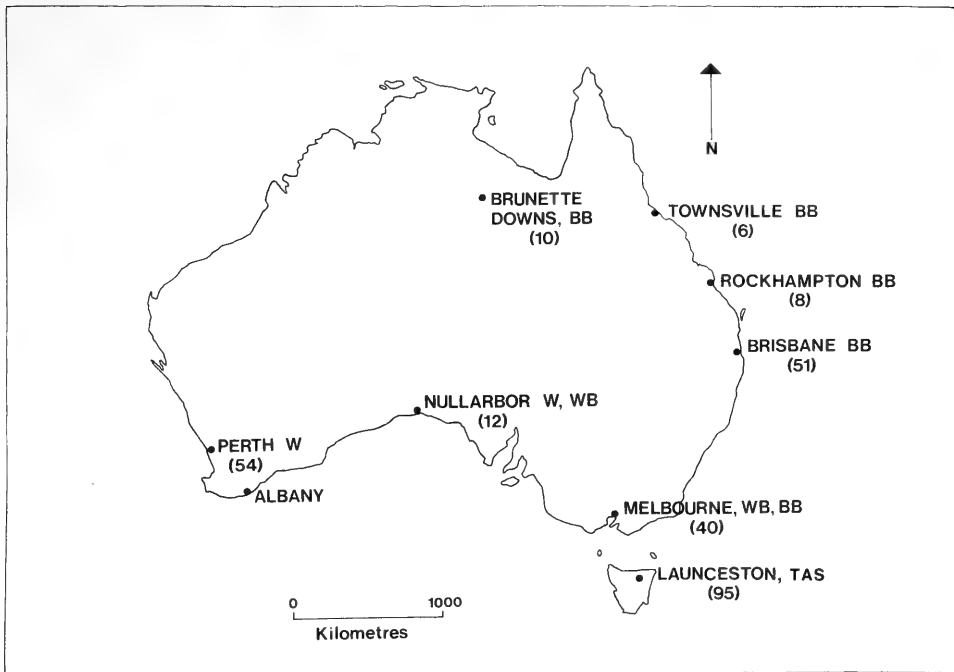


Fig. 1. Map of Australia showing areas sampled for magpie lice. Letters after place names indicate the types of magpies sampled in those areas. BB: Black-backed, W: Western, WB: mainland white-backed, Tas: Tasmanian white-backed. Numbers below place names indicate the number of magpies examined.

Only the results of *Philopterus* sp. and *Bruelia* sp. were analysed further because individuals belonging to the genus *Myrsidea* are fast moving and very difficult to catch. It was not always possible to determine with any certainty whether or not *Myrsidea* were present on the birds.

ANALYSIS

For each host-type (i.e. white-backed, black-backed, western or Tasmanian), the percentage of birds infested with each species was calculated. The mean number of lice per bird was also calculated. However, the standard deviations were larger than the means, due to the high number of zero values in the data; and it was not possible to compare statistically the means for each host-type. The test of proportions (Freund 1979) was used to compare the percentage of each host-type infested with each species of louse. In order to examine the possibility of any difference between host-types being solely due to differences in host plumage colour, westerns were subdivided into males (white-backed) and immatures and females (black-backed) and their rates of infestation compared. Some reports, however, suggest that juveniles may be either more heavily (Clay 1958) or less heavily (Ash 1960) infested with lice than adults. Therefore the procedure was repeated using only adult males and females.

Because there appeared to be seasonal variations in lice density, the hosts were then grouped according to the month of capture and the proportion of birds infested

TABLE 1. Mean number of each genus of Ischnocera per bird and the percentage of magpies infested.

	<i>Philopterus</i>	<i>Bruelia</i>	Statistical Test used	Significance level
mean number per bird	0.58	1.59	t test	n.s.
standard deviation	2.47	5.35		
% of birds infested	6.16	25.36	test of proportions (Freund 1979)	p<0.001
sample size	276	276		

was calculated for each month. The test of proportions was used to determine whether there were significantly higher infestations in any one month compared to any other month. The purpose of this part of the study was to ensure that differences in lice infestations between host-types and/or areas were not merely reflections of seasonal variations, influenced by the times at which specimens were collected.

RESULTS

Table 1 shows the percentage of birds infested with Ischnocera, and the proportion infested with *Bruelia* was significantly higher than the proportion infested with *Philopterus* ($p < 0.05$). This result is possibly an underestimate, due to *Philopterus* being more visible.

Also there seem to be differences in densities between *Philopterus* and *Bruelia*, but differences were not significant because of the huge variations in number of lice per bird. Numbers of *Bruelia* per host ranged from zero to over 500 and numbers of *Philopterus* per host ranged from zero to over 70.

TABLE 2. Percentage of magpies of different types infested with Ischnocera. Comparisons are between host-types for each genus of Ischnocera. Within each genus, samples with similar superscripts are not significantly different ($p > .05$).

Host-type	N	% of magpies infested	
		<i>Philopterus</i>	<i>Bruelia</i>
mainland white-backed	40	15.00 ^b	12.50 ^a
black-backed	77	6.49 ^{ab}	40.26 ^b
western	64	6.25 ^{ab}	14.06 ^a
Tasmanian white-backed	95	2.11 ^a	26.32 ^{ab}
all mainland birds	181	8.29 ^b	24.86 ^{ab}

Only the white-backed mainland birds and Tasmanian birds had significantly different percentage infestations of *Philopterus*, with the proportion of white-backed mainland birds being significantly higher than for Tasmanian birds (Table 2). When the results for all mainland birds were pooled a significantly higher proportion of mainland birds than of Tasmanian birds were infested with *Philopterus*. For *Bruelia*, infestations of mainland white-backed birds were significantly lower than those of black-backed birds. Also, the proportion of black-

backed birds infested was significantly higher than the proportion of western birds infested. There were no other significant differences between host-types in regard to percentage of birds infested.

Because white-backed magpies appeared to have a lower proportion of birds infested with *Bruelia* than black-backed birds, the two sexes of the western form (which has white-backed males and black-backed females) were compared to determine whether infestation levels differed between them. This could occur if back-colour was important in determining survival rates or reproductive rates. For example, black feathers would absorb more heat than white feathers and therefore the environment on the back of a black-backed bird may be slightly warmer than that on a white-backed bird. This could cause an increase in growth and reproductive rates. Alternatively, the lice, which are dark brown in colour, may be more easy for the host to see, and therefore pick off, on white feathers than on black feathers. In general lice tend to be similar in colour to the feathers on which they life (Eichler 1948).

The alternatives are that, either reproduction may be faster on black-backed birds, or survival rates may be lower on white-backed birds or colour may be unimportant. To examine this, infestation of western magpies were analysed. Results of both these analyses are shown in Table 3. The proportion of birds infested was higher for females and young, and females alone than for adult males, although these differences were not significant. The small sample sizes may have been responsible for the non-significant results.

TABLE 3. Percentage of western magpies infested with *Bruelia*.

Females, immatures and juveniles combined		Adult females		Adult males	
%	N	%	N	%	N
20.00	35	11.76	17	8.33	12

The seasonal variation in percentage of birds infested is illustrated in Fig. 2. The highest infestations of *Philopterus* appear to be in July with much lower infestations in the other months. Infestations of *Bruelia* are highest between April and June.

Very few months had significantly different (at the .05 level) levels of *Philopterus* infestation (Fig. 2). July had significantly higher levels of infestation than most other months. January infestations were significantly lower than April, May, June, July, August, November and December infestations and August, September, October, November and December infestations were lower than those in April and May. No birds were caught in February and March.

DISCUSSION

The results suggest that a higher proportion of birds are infested with *Bruelia* than with *Philopterus* (significant at .05 level) and that the mean number

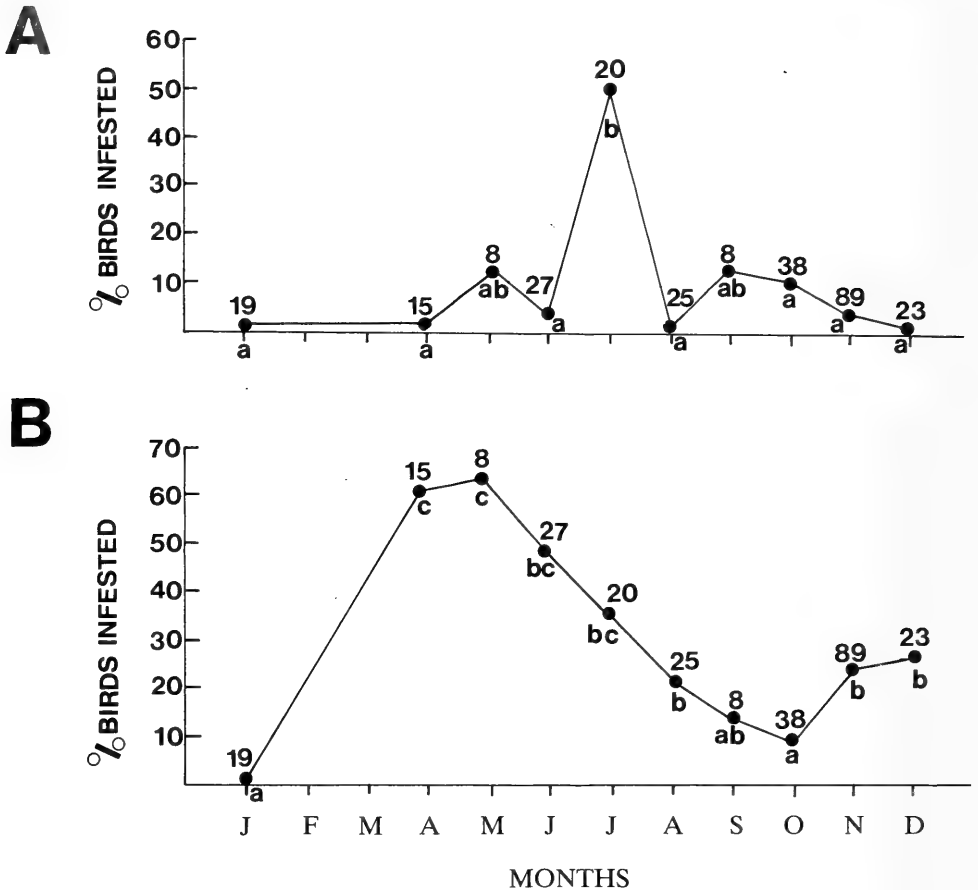


Fig. 2. Seasonal variations in infestation rates. A. *Philoaterus*, B. *Bruelia*. Numbers above points indicate the number of birds examined. Any two points with the same letter beneath them were not significantly different in the percentage of birds infested.

of *Bruelia* per bird is higher than the mean number of *Philoaterus* per bird (although this difference was not significant because of the high number of zero values). This result differs from reports by Ash (1960), who found *Philoaterus* and *Bruelia* occurring with equal frequency on 54 blackbirds. No doubt there is much variation between host-types in relative frequencies of the various genera of Mallophaga, even though the same two genera may be present in each case.

Significantly fewer Tasmanian than mainland birds (treated as a whole) were infested with *Philoaterus*. Only two Tasmanian birds of 95 examined by the author and a further 40 birds examined by Mr R. H. Green (of the Queen Victoria Museum, Launceston) were found to harbour any *Philoaterus*. Both

of these birds belonged to the same territorial group, one probably being the offspring of the other. From Table 2 it can be seen that if the mainland birds are divided into host-types only the mainland white-backed birds, which geographically are closest to the Tasmanian birds have significantly higher *Philopterus* infestations than Tasmanian birds. A study of morphometric differentiation among *Philopterus* populations on different magpie host-types showed that the Tasmanian individuals were distinct from mainland forms (Hughes 1980). Possibly these individuals belong to a distinct species or geographic race which may have different reproductive rates and/or dispersal abilities from mainland forms, which would result in different rates of infestation.

The white-backed mainland magpies had significantly lower infestations of *Bruelia* than black-backed magpies. However, when young and adult female westerns were compared with adult male westerns, no significant differences were found in proportion of birds infested with *Bruelia*, although females and immatures were approximately twice as heavily infested as adult males. The small number of adult males and adult females examined were probably responsible for the lack of any significant difference. This suggests that differences in levels of *Bruelia* infestation between black-backed and white-backed birds may be a result of the back colour. The observation that males have a lower frequency of infestation than females is contrary to Ash's report that males are slightly more heavily infested than females (Ash 1960). Therefore the lower level of infestation in males in the western magpie cannot be explained as a general sex trend.

The seasonal variations in louse infestations differ between the two genera (Ash 1960; Foster 1969). In *Philopterus* the peak occurs just prior to the breeding time of the hosts, i.e. July to September (Carrick 1972). This increase in infestation prior to breeding has been observed by other authors (Ash 1960, Foster 1969). According to Foster (1969), louse breeding usually occurs just prior to the bird breeding time, so that there are large numbers of young ready to transfer to the young hosts in the nests. In *Bruelia* the peak appears to be much earlier than the breeding time of the host.

To conclude, it seems that there is a higher frequency of *Bruelia* than *Philopterus* infestations. The proportion of Tasmanian birds infested with *Philopterus* is lower than mainland birds. It is possible that this is due to differential selection between the two populations but *Philopterus* live mostly on the nape of their host which is white in all host-types and therefore the habitats provided by the different host-types must be very similar. Possibly the Tasmanian magpies which are distinct from mainland birds on morphometric and biochemical characters (Hughes 1980) provide a slightly less favourable habitat than mainland birds for *Philopterus*. Alternatively the *Philopterus* found on Tasmanian magpies may be a distinct species or geographic race, which has lower reproductive rates and/or dispersal abilities than the mainland form and therefore infests fewer birds.

The difference in *Bruelia* infestation between white-backed and black-backed birds could be due to differing survival on the two colour types. Black feathers may provide a more suitable habitat for *Bruelia* than do white feathers.

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Morphometric Variation in the Mallophaga of the Australian Magpie (*Gymnorhina tibicen* Latham)

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ABSTRACT

Ischnocera were collected from live and road-killed Australian magpies in order to examine morphometric variation between lice from different host-types. Lice from the body (*Bruelia* sp.) showed little variation between host-types, but lice from the neck (*Philopterus* sp.) of Tasmanian magpies were quite distinct from those from mainland magpies. There was some differentiation between *Philopterus* from different mainland magpie populations, but differences were not consistent between males and females. These relationships correlate well with those described for the hosts.

INTRODUCTION

Members of the order Mallophaga are unusual among parasitic insects in that they can spend their whole life-cycle on a single bird host (Clay 1958). It has been suggested that, usually, bird lice only transfer between hosts when they come into close contact, such as when mating, nesting or roosting (Clay 1950). If so, then louse populations on a particular bird species will be effectively geographically isolated from louse populations on other bird species, a situation which could theoretically lead to speciation (Mayr 1970). According to Mallophagan taxonomists (e.g. Harrison 1914, Hopkins 1941, Clay 1958) this restricted movement of bird lice between hosts has led to a close correlation between bird and Mallophagan phylogenies. In fact, it has been suggested that Mallophagan phylogenies may aid in bird classification, particularly at the level of order, family and genus (Clay 1958).

The aim of the present study was to determine whether a similar correlation to that observed at the order and family level (Clay 1958) existed at the population and species level. In particular I was interested in relationships between bird lice from different populations of the Australian Magpie (*Gymnorhina tibicen*).

The taxonomic status of the Australian Magpie has long been a matter of debate (e.g. Campbell 1929, Amadon 1951, Slater 1974). There are three distinct colour forms in the species *G. tibicen*. A black-backed form inhabits northern and

central Australia. A white-backed form is found in the south-east of Australia, including Tasmania, and in some highland areas of New South Wales and central Australia. A third form, where the male is white-backed and the female is black-backed, inhabits the south-western part of Australia (Slater 1974). Morphometric, biochemical and behavioural investigations suggest that all mainland forms belong to a single polymorphic species and that the Tasmanian form, if not a separate species, is certainly the most divergent population (Hughes 1980, 1982).

Three genera of Mallophaga are commonly found on magpies. Two of these, *Philopterus* and *Bruelia*, belong to the superfamily Ischnocera, family Philopteridae, while the third genus, *Myrsidea*, belongs to the superfamily Amblycera, family Menoponidae. Members of the latter superfamily are very fast-moving, are relatively non habitat-specific and leave the host soon after it dies. The genus *Myrsidea*, compared to the two Ischnoceran genera, is relatively uncommon on magpies, was difficult to catch on live birds and could not be collected from dead birds. It was omitted from the study. *Philopterus* is found only on the head and neck of the bird, while *Bruelia* occurs mostly on feathers of the back, wings and abdomen. Both forms are slow moving and easily caught, remaining on dead birds for up to a week.

The aim of the present study was to carry out a morphometric study of the lice to determine whether relationships between Mallophagan populations reflected those between their hosts. The species of *Philopterus* from magpies is undescribed and will be referred to as *Philopterus* sp. *Bruelia semiannulata* is the only member of the genus described from *Gymnorhina* and all populations examined here belonged to this species.

MATERIALS AND METHODS

COLLECTION

Magpies were trapped using a caged decoy inside a wire trap, with a funnel entrance at one end. An assistant was required to hold each bird while it was examined for lice. Each feather on the head, neck and back was searched and all adult lice were collected and stored in 70% alcohol. Breast and abdomen feathers were also examined, but lice were rarely found. Samples were also collected from road-killed magpies, which were thoroughly examined and from which all live lice were collected. Additional specimens of lice were borrowed from Professor R. Pilgrim (Canterbury University, New Zealand), Mr R. H. Green (Queen Victoria Museum), and Miss T. Clay (British Museum of Natural History). Attempts were made to collect lice from at least 2 localities for each magpie form (i.e. white-backed, black-backed and western). However, this was not always possible as many birds examined produced no lice. Specimens of *Philopterus* were particularly difficult to collect in large numbers. Localities from which magpie lice were sampled are shown in Fig. 1.

PREPARATION AND MEASUREMENT OF SPECIMENS

Specimens were soaked in 10% KOH for 48 hours and then mounted in Canada Balsam using the method of Pilgrim (1977). Head characters shown in Figs. 2 and 3 were measured using a Swift Ocular Micrometer No. 5 in the eyepiece of an Olympus

VARIATION IN MAGPIE MALLOPHAGA

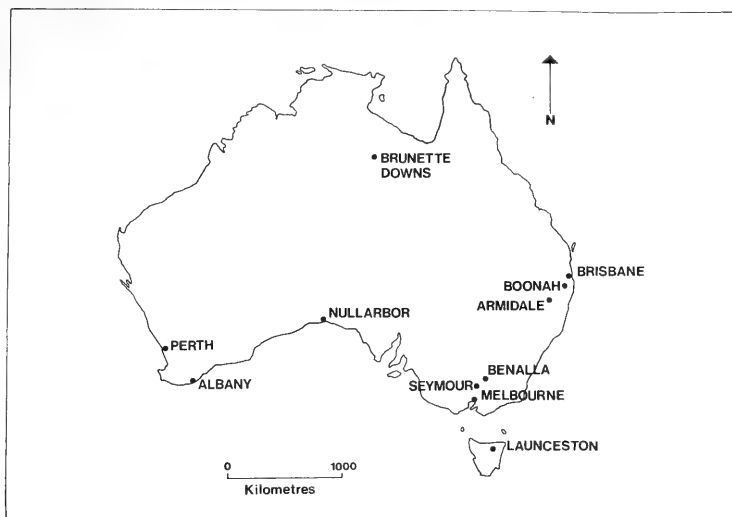
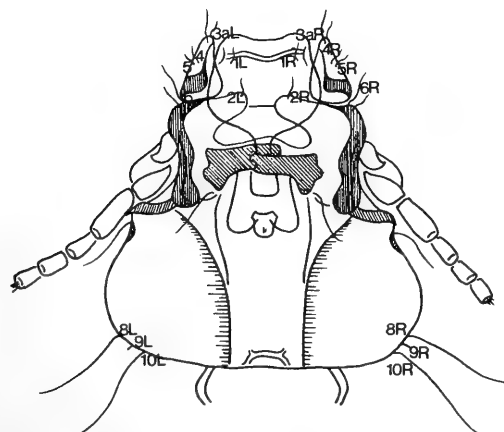


Fig. 1. Map of Australia showing localities from which magpie lice were collected.

monocular microscope. Only head measurements were made because (a) the head characters (particularly the chaetotaxy) of Mallophaga have been widely used in traditional taxonomic studies and have been found very useful for differentiating between species, and (b) because the lice were soaked in KOH, some of the body parts became softened. The head is very chitinous and retains its shape, even after 96 hours in KOH, whereas the abdomen can lose its shape after exposure to KOH.

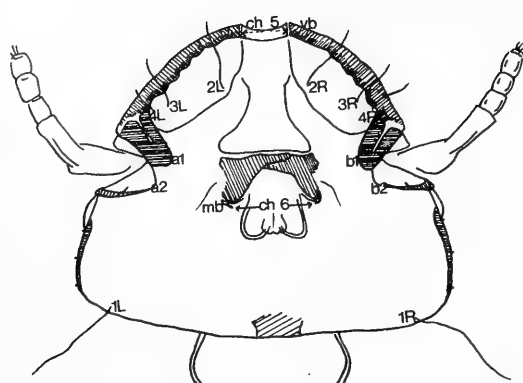
ANALYSIS

Only adults were used and males and females were analysed separately because sexual dimorphism is common in Mallophaga (Eichler 1938, Clay 1958). For each analysis



Character No.	Character Description
1	base of 1L to base of 1R
2	base of 2L to base of 2R
3	base of 2aL to base of 3aR
4	base of 4L to base of 4R
5	base of 6L to base of 6R
6	base of 8L to base of 8R
7	base of 9L to base of 9R
8	base of 10L to base of 10R
9	base of 2L to base of 3L
10	base of 4L to base of 4L
11	base of 2L to base of 5L
12	base of 3L to base of 5L
13	base of 3L to base of 6L
14	head length in median line

Fig. 2. Head of *Philopterus* showing characters measured for morphometric analysis.



Character No. Character Description

- 1 base of 1L to base of 1R
- 2 base of 2L to base of 2R
- 3 base of 3L to base of 3R
- 4 base of 4L to base of 4R
- 5 distance between edges of ventral band (vb)
- 6 distance between mandible bases (mb)
- 7 distance from a1 to b1
- 8 distance from a2 to b2
- 9 head width posterior to antennae
- 10 head width at widest part
- 11 head length in median line
- 12 base of 2L to base of 3L
- 13 base of 3L to base of 4L

Fig. 3. Head of *Bruelia* showing characters measured for morphometric analysis.

the original data was standardised by mean and standard deviation (Sneath and Sokal 1973). A distance matrix of squared Euclidean distances between each pair of individuals was then calculated. In order to identify groupings according to the characters measured, a principal coordinates analysis (Gower 1966) was performed on the matrix, using the programs MULCLAS and GOWER, from the CSIRO statistical package TAXON, on the Cyber 76 computer Canberra. This produces an ordination of all individuals on transformed or principal axes. The first principal axis produces the greatest separation between all individuals. The second principal axis is perpendicular to the first and produces the next greatest amount of separation, and so on. Usually the first two axes account for more than 50% of the total variation, so that it is possible to visualise the separation by plotting the first two principal axes against one another.

Canonical variates analysis was also performed on each genus. This method is described by Blackith and Reyment (1971) and has been used extensively by biologists for discriminating between taxonomic groups (e.g. Blackith and Blackith 1969, Phillips et al. 1975). Basically, the method involves the computation of transformed axes, as for principal coordinates analysis. In canonical variates analysis, however, the axes are in the direction producing the greatest variability between the means of the groups (rather than the individuals, as in principal coordinates).

For *Phlopterus*, separate analyses were performed, one grouping individuals according to locality and the other grouping individuals according to the back colour of their host. *Bruelia* individuals were grouped according to host back colour. Due to the low level of separation, further analyses were not performed.

* Boonah	black-backed	● Seymour	white-backed
* Benalla	black-backed	⊗ Nullabor	western/white-backed
☆ Perth	western	○ Brunette Downs	black-backed
■ Albany	western	● Launceston	white-backed
◇ Armidale	black-backed		

Fig. 4. Principal coordinates plots showing relationships between *Phlopterus* from different localities and host-types. a. Females; b. Males.

VARIATION IN MAGPIE MALLOPHAGA

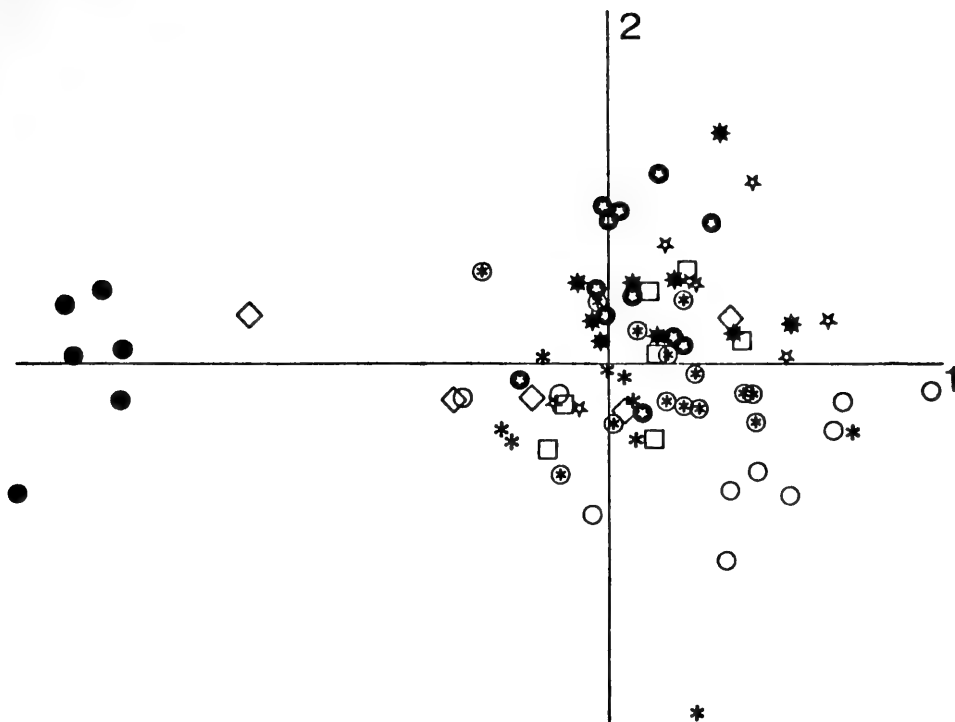


Fig. 4a

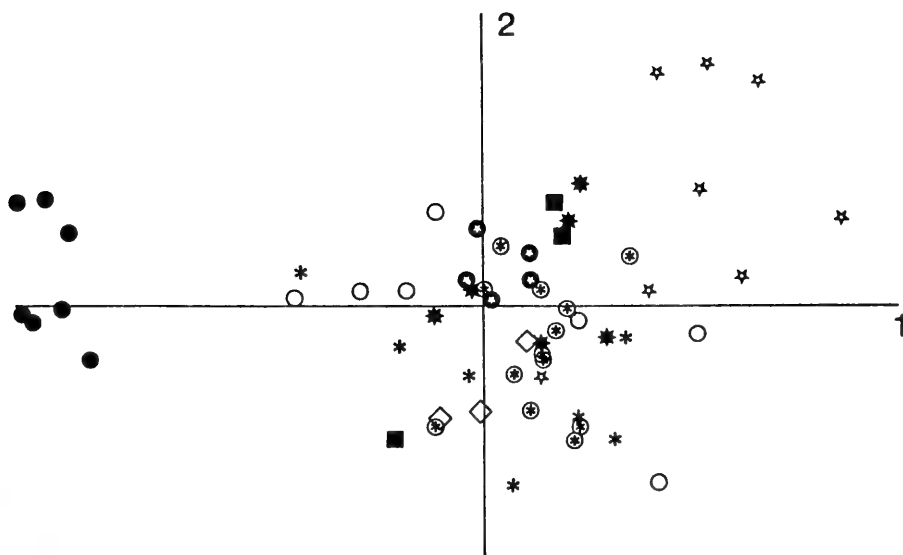


Fig. 4b

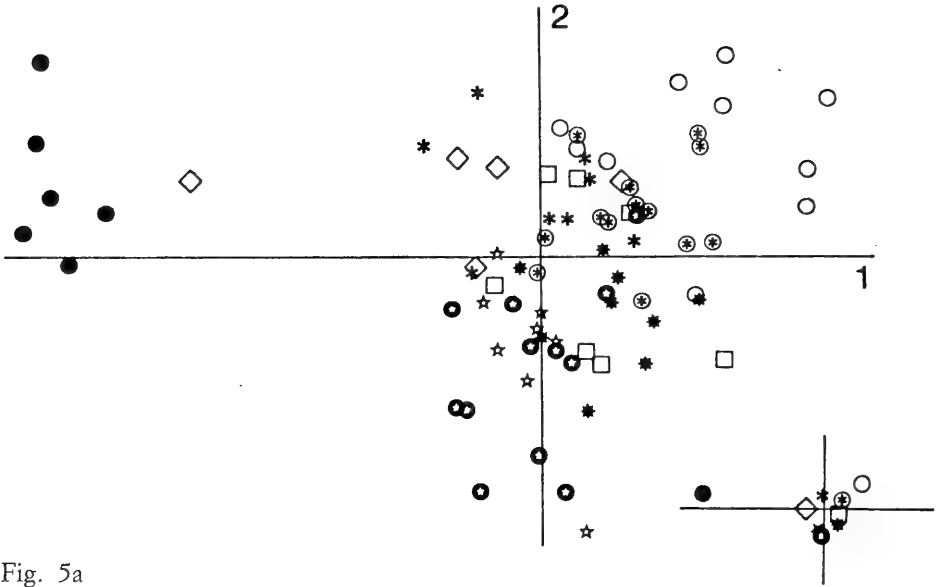


Fig. 5a

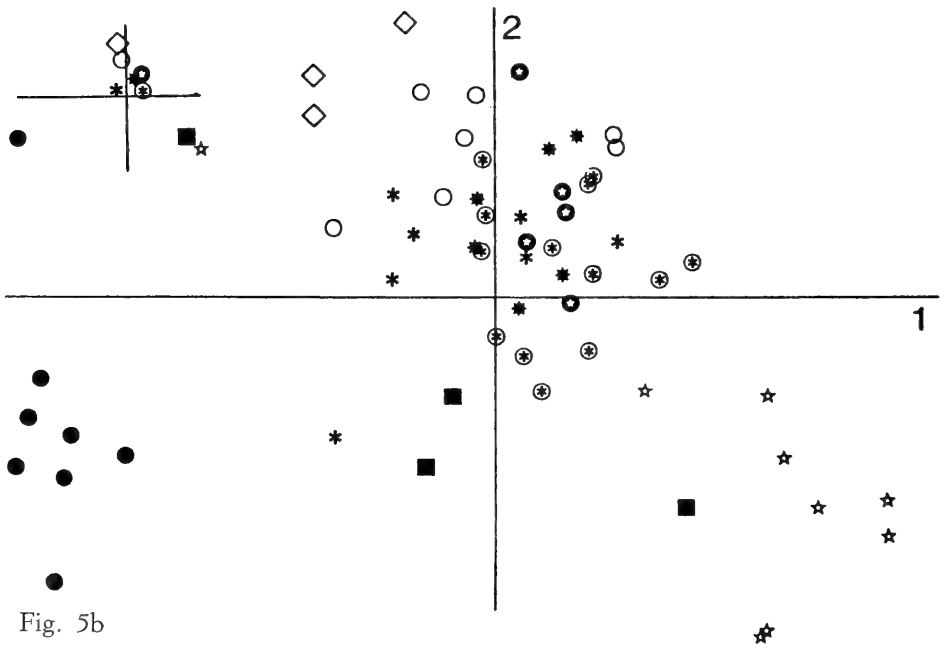


Fig. 5b

Fig. 5. Canonical variates plots showing relationships between *Philopterus* from different localities. Individuals are plotted on the large axes and the means for each locality are shown on the smaller axes. a. Females; b. Males.

RESULTS

Philopterus

The results from the principal coordinates analysis on females are shown in Fig. 4a, where the first two axes are plotted against each other. The Tasmanian individuals are quite distinct from all mainland lice, with only a single individual from Armidale anywhere near them on the plot. There is no separation between mainland groups, although the Brunette Downs individuals are mostly in the bottom right hand corner. The south-eastern Australian individuals (i.e. from Benalla, Seymour and Melbourne) are mostly in the top half of the graph, but there is considerable overlap with Perth, Boonah and Nullabor individuals. There is no separation between south-eastern individuals according to the back colour of their hosts (i.e. lice from Benalla black-backed birds overlap with white-backed birds from Seymour and Melbourne).

The plot for males (Fig. 4b) shows a similar result. The Tasmanian lice are again quite distinct from all mainland lice. Apart from Perth individuals, which overlap only slightly with other lice, there seems to be no separation between mainland lice according to locality.

Figs. 5a and 6a plot the results from canonical variates analyses performed on *Philopterus* females. In Fig. 5, individuals are grouped according to locality and in Figure 6 they are grouped according to the back colour of their host. In both graphs, Tasmanian individuals are distinct, but overlap occurs between mainland groups.

Results for canonical variates analyses on males are illustrated in Figs 5b and 6b. Tasmanian individuals are distinct in both plots. There appears however to be some separation between mainland lice from different localities. Perth lice are almost distinct, overlapping only with one of the Albany individuals and the three Armidale individuals do not overlap with any of the others. When lice are grouped according to host back colour, no separation between back colours is evident.

Bruelia

Figs. 6c and 6d show results of canonical variates analysis on *Bruelia* females and males respectively. In both cases, there was overlap between individuals from the four host-types, although in the males, there appeared to be some differentiation of Tasmanian individuals.

DISCUSSION

Apparently little differentiation exists between mainland populations of lice on magpies, either in *Bruelia* or in *Philopterus*, although *Philopterus* appears to show some differentiation between populations. The results, however, differed between males and females (Figs. 4 and 5). In the females the most distinct populations appeared to be from Boonah and Brunette Downs magpies, while in

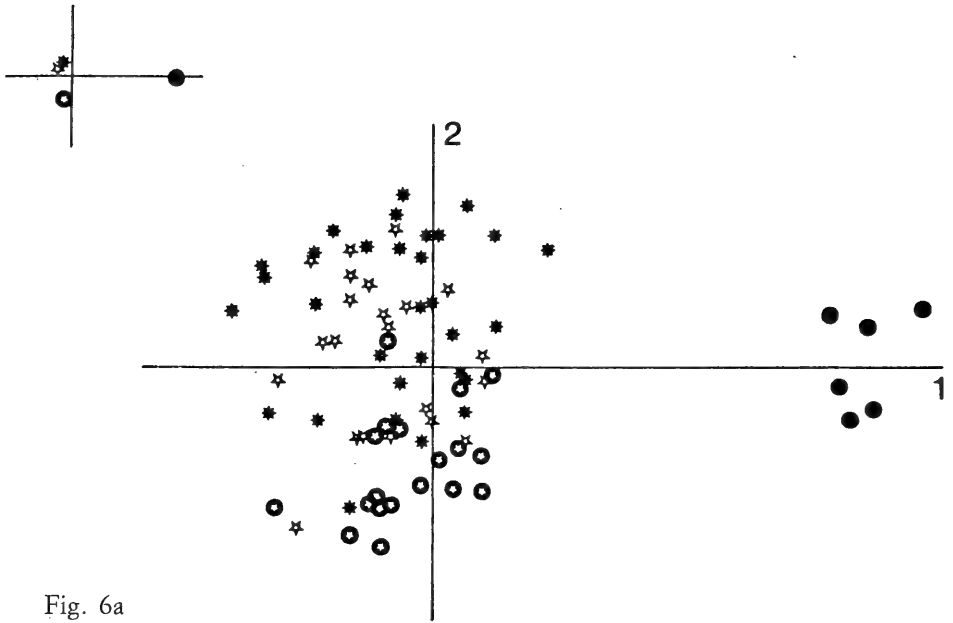


Fig. 6a

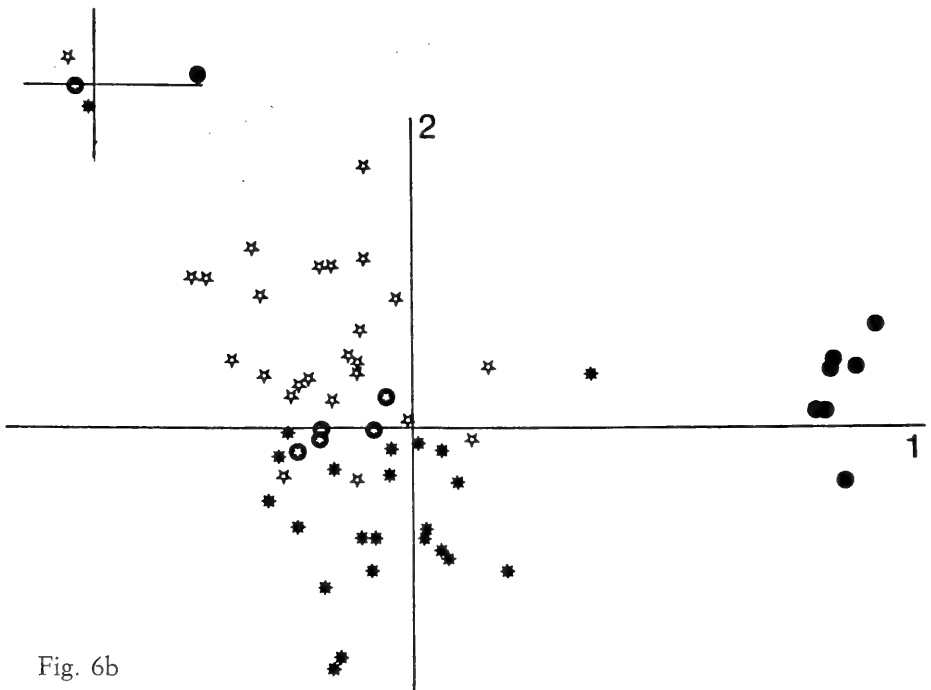


Fig. 6b

VARIATION IN MAGPIE MALLOPHAGA

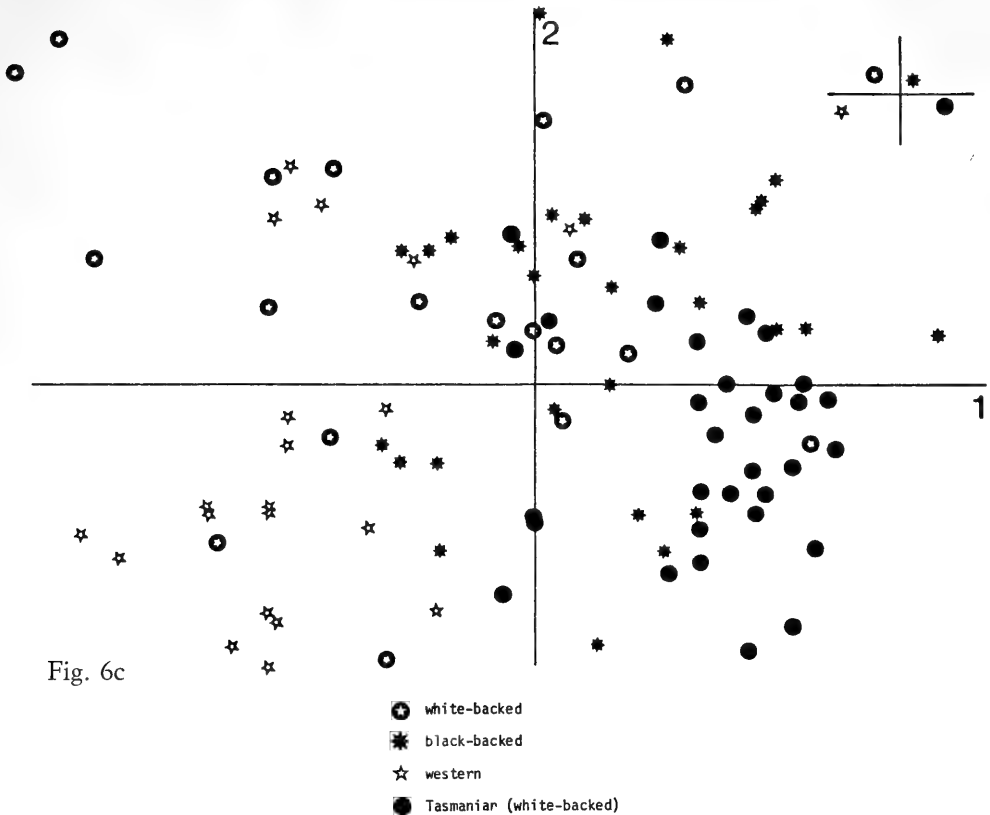


Fig. 6. Canonical variates plot, showing relationships between lice from different host-types. Individuals are plotted on the large axes and the means for each host-type on the smaller axes. a. *Philopterus* females; b. *Philopterus* males; c. *Bruelia* females; d. *Bruelia* males.

the males, lice from Perth, Armidale and Benalla magpies were most distinct. These results probably reflect the arbitrary nature of the grouping and therefore little reliability can be placed on them. Only the separation of Tasmanian lice was observed in both sexes, which suggests complete isolation, in terms of the characters measured.

Philopterus exhibits greater divergence between populations than does *Bruelia*. Clay (1958) observed that *Philopterus* varied more between host species than did *Bruelia*, so the greater between population variation of *Philopterus* was not unexpected. The reasons for this difference are not clear but could be due to greater habitat specificity of *Philopterus* [suggested by Clay (1958)] or different rates of movement between hosts in the two genera.

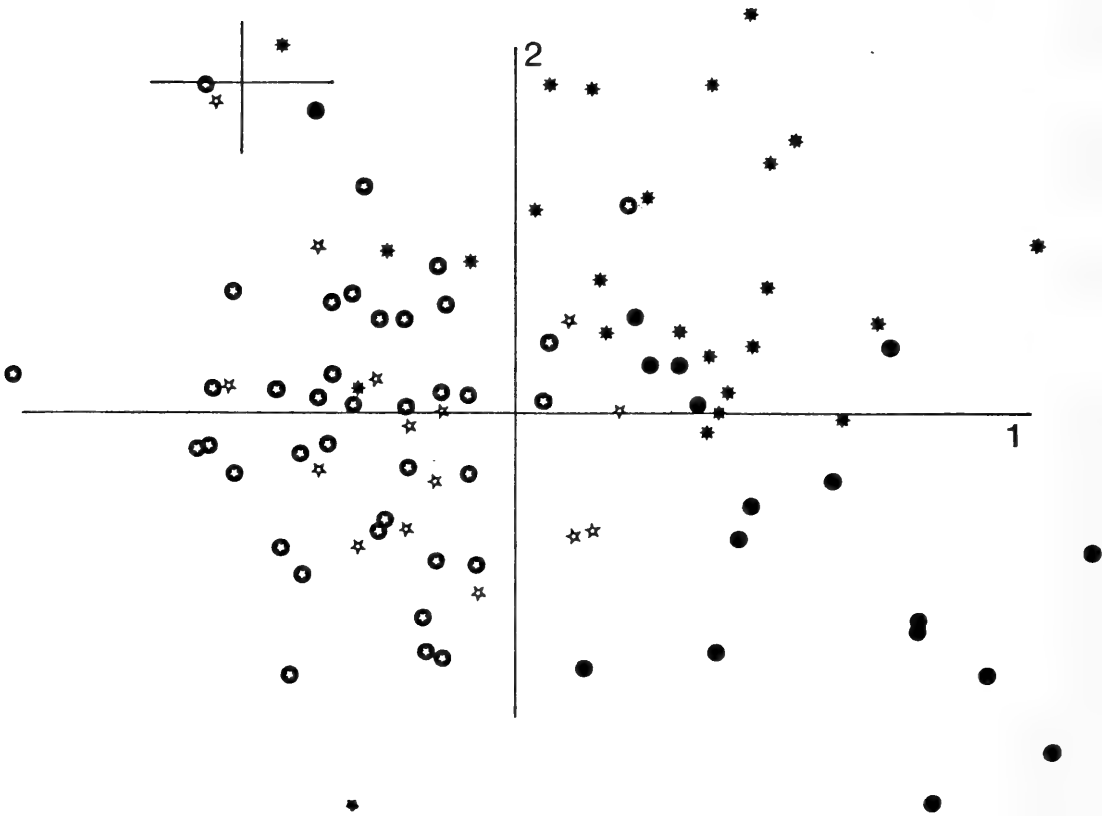


Fig. 6d

Results from the morphometric analysis of the lice correlate well with those described earlier for magpies. Very little differentiation occurs between mainland populations in either *Philopterus* or *Bruelia*. There seems to be no differentiation between lice from white-backed, western or black-backed magpies. As in the magpies however, the Tasmanian *Philopterus* are distinct from mainland populations. The fact that *Philopterus* seems to reflect more exactly relationships between host populations suggests that this genus may be more useful than *Bruelia* as an aid to understanding bird phylogeny. Certainly within host-species, *Bruelia* shows very little differentiation.

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Two New Species of *Pseudomugil* (Pisces: Melanotaeniidae) from Irian Jaya and New Guinea

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ABSTRACT

Two new species of *Pseudomugil*, *P. helodes* from Misool and Batanta Islands, Irian Jaya and *P. majusculus* from North New Guinea, are described on the basis of specimens obtained by the Alpha Helix Expedition in 1979. *Pseudomugil helodes* appears to have no close relatives, but belongs to a species complex which includes *P. signifer*, *P. gertrudae* and *P. tenellus*. *Pseudomugil majusculus* is also a member of this group and is most closely related to *P. signifer* of eastern Australia. A key to the genus *Pseudomugil* is included.

INTRODUCTION

Munro (1958, 1967) listed four species of *Pseudomugil* from Australia and five species from New Guinea. *P. gertrudae* was included in both lists on the basis of its distribution on both sides of Torres Strait. Further collecting in recent years has resulted in description of four additional species (Taylor 1964, Roberts 1978, Allen and Moore 1981, Allen and Ivantsoff 1982). Comprehensive studies of Melanotaeniidae by Allen (1980) and Allen and Cross (1982) had shown that *P. furcatus* Nichols from northern New Guinea merits generic distinction. In addition, *P. signatus* (Günther) was recognised as a junior synonym of *P. signifer* by Hadfield *et al.* (1979). The species recognised by the present authors include: *P. gertrudae* Weber (New Guinea and Australia), *P. inconspicuus* Roberts (New Guinea), *P. mellis* Allen and Ivantsoff (Australia), *P. novaeguineae* Weber (New Guinea), *P. paludicola* Allen and Moore (New Guinea), *P. signifer* Kner (Australia) and *P. tenellus* Taylor (Australia). Two additional species, *P. helodes* from Irian Jaya and *P. majusculus* from New Guinea are described herein. These new species were collected during the 1979 "Alpha Helix" Expedition to Indonesia and New Guinea by Dr Bruce B. Collette.

MATERIALS AND METHODS

The methods for counts and measurements are mainly based on Munro (1967) with the exception of the following: the interdorsal scale count was taken from the origin of the last spine of the first dorsal fin along the mid-dorsal line to the origin of the

first element of the second dorsal fin. The predorsal scale count included all the scales along the mid-dorsal line from the head to the origin of the first dorsal. The transverse scale count was taken by counting rows of scales diagonally downwards and forwards from the origin of the first dorsal fin to and including the midlateral scale row, plus the scales counted diagonally upwards and backwards to the lower edge of the midlateral row, from the origin of the ventral fins. The midlateral scale count was taken as the number of scales between the upper pectoral fin base and the hypural joint. The position of the origin of the first dorsal fin was recorded as a number of scales in front of a vertical through the pelvic fin tips and also as the number of scales behind a vertical through the pectoral fin tips. The position of the origin of the ventral fins was recorded as a number of scales in front of or behind a vertical through the pectoral fin tips. The position of the second dorsal fin was recorded as a number of scales behind a vertical through the origin of the anal fin. All measurements were made to the nearest 0.1 mm with dial calipers. Standard length is abbreviated as SL. Measurements and counts were recorded for 30 type specimens of *P. helodes*. *Pseudomugil majusculus* is described from the holotype which is the only known specimen. Line drawings of the mouth parts of *P. signifer*, *P. helodes* and *P. majusculus* were made from prepared alizarins (with the exception of the last species) using camera lucida.

Specimens of *P. helodes* are deposited at the United States National Museum of Natural History (USNM), The Australian Museum Sydney (AMS) and Western Australian Museum, Perth (WAM). The holotype of *P. majusculus* is deposited at USNM. The following specimens were studied for comparative purposes:

P. inconspicuus, 25 specimens (USNM 217162, holotype and USNM 21763, paratypes).

P. novaeguineae, ZMA 103.197 (Zoological Museum of the University of Amsterdam, specimen labelled lectotype); ZMA 110.175 (2 specimens labelled paralectotypes); ZMA 103.198, 6 specimens.*

P. paludicola, 10 specimens (AMS I.21302-001, paratypes).

P. gertrudae, ZMA 103.196 (5 specimens labelled paralectotypes); SMF 10013 (Senckenberg Museum, Frankfurt, 4 of 12 specimens, all labelled paratypes).*

P. signifer, MU I.081 (Macquarie University Sydney), 5 specimens; MU I.143, 5 specimens; 422 specimens (see Hadfield *et al.*, 1979).

P. tenellus, 13 specimens (USNM 174252, paratypes).

* The validity of the status of some of the type specimens appears to be doubtful and will require an investigation.

KEY TO SPECIES OF *PSEUDOMUGIL*

Allen and Cross (1982) presented a key and diagnoses for the known species of *Pseudomugil*. The acquisition of additional material and descriptions of *P. mellis* by Allen and Ivantsoff (1982) and the two species described herein is justification for a revised key which appears below.

- 1a. First dorsal origin at or behind vertical through origin of ventrals; predorsal scale count rarely as low as 13 and usually more than 15 2
- 1b. First dorsal origin in front of vertical through tips of ventrals; predorsal scale count rarely as high as 14 and usually less than 13 4
- 2a. First dorsal origin in front of vertical through origin of anal; mouth gape wide and completely unrestricted *P. novaeguineae*

NEW SPECIES OF *PSEUDOMUGIL*

- 2b. First dorsal origin behind vertical through origin of anal; mouth gape small and restricted by ligament 3
- 3a. No conspicuous lateral process on premaxillary bone; anal fin ray count 10-14; least depth in SL 6.7-8.0 *P. paludicola*
- 3b. Pungent lateral process on premaxillary; anal fin ray count 9-11; least depth in SL 9.2-11.0 *P. inconspicuus*
- 4a. Unpaired fins with round or oval spots on median fins; pectoral fins with orange tinge in live males, clear in females *P. gertrudae*
- 4b. Unpaired fins coloured or clear but never with oval spots; pectoral fins clear irrespective of sex 5
- 5a. Gill raker count in first lower gill arch 12 or less 6
- 5b. Gill raker count in first lower gill arch 14 or greater 7
- 6a. Unpaired fins usually whitish in outline in males but clear in females when live; transverse scale count 7-9; anal fin ray count 6-8 *P. tenellus*
- 6b. Unpaired fins with black, yellow or orange markings in males and translucent in females; transverse scale count 5-6; anal fin ray count 9-12 8
- 7a. Gill rakers in first lower gill arch 16-18; midlateral scales 28-30; body scales distinctly crenulated *P. belodes*
- 7b. Gill rakers in first lower gill arch 14; midlateral scales 26; scales not crenulated *P. majusculus*
- 8a. Pores small on head and absent on lower jaw; teeth in upper jaw small and not visible when mouth closed. Interorbital width in head 2.4-3.2, usually nearer 3.2 *P. mellis*
- 8b. Pores large on head and present on lower jaw; teeth in upper jaw large and distinctly visible when mouth closed. Interorbital width in head 1.9-2.5, usually nearer 2.3 *P. signifer*

PSEUDOMUGIL HELODES, NEW SPECIES

Pseudomugil species "A" Allen and Cross, 1982: 130.

Holotype — USNM 236543, 27 mm, rotenone in 1 m of water, in mangrove swamp, Misool Island, Irian Jaya, Indonesia, 02° 3.1'S 130° 6.4'E, 3 July, 1979, collected by Bruce B. Collette "Alpha Helix" Expedition, 1979.

Paratypes — 31 specimens: USNM 236545, 21 specimens, 19.7-25.7 mm SL, data as for holotype; USNM 236544, 7 specimens, 17.9-29.6 mm SL, rotenone in 1m of water, in mangrove swamp, Batanta Island, Marchesa Bay, North West Irian Jaya, Indonesia, 0°48.2'S 130° 52.8'E, 2 July, 1979, collected by Bruce B. Collette, "Alpha Helix" Expedition, 1979. AMS I.24364-001, 2 cleared and stained specimens, 20.0-25.6 mm SL, data as for holotype.

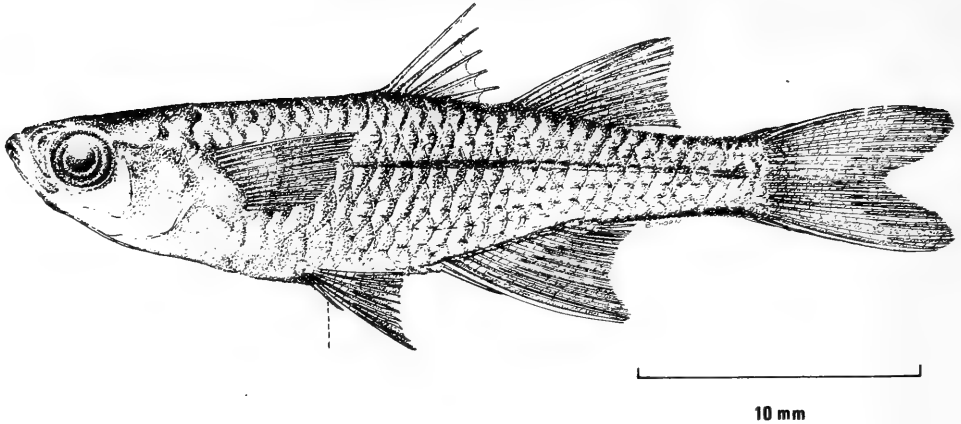


Fig. 1. *Pseudomugil helodes*, line drawing of the holotype USNM 236543, 27 mm SL.

Other specimens — AMS I.22838-001, 5 specimens, 17.9-20.0 mm SL, data as for holotype; WAM P27972-001, 5 specimens, 17.7-21.6 mm SL, data as for holotype; USNM 236546, 12 specimens, 11.6-19.7 mm SL, data as for holotype.

The description of the new species is based on the holotype and paratypes.

GENERAL DESCRIPTION

Meristics and Morphometrics

All of the measurements and counts taken are presented in Table 1.

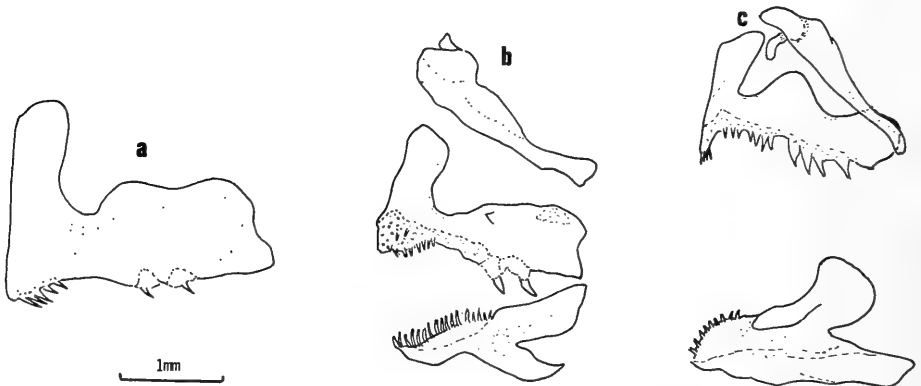


Fig. 2. a. Premaxillary bone of the holotype of *Pseudomugil majusculus* USNM 236542, 3.2 mm SL.
 b. Maxilla, premaxilla and dentary of *Pseudomugil signifer*, an unregistered alizarin specimen, Smith Lake, N.S.W. Australia, 32°23'S 152°28'E, 27 mm SL.
 c. Maxilla, premaxilla and dentary of *Pseudomugil helodes*, USNM 236545, 26.8 mm SL.

NEW SPECIES OF *PSEUDOMUGIL*

TABLE 1. Measurements and counts of 30 specimens of *Pseudomugil helodes*. Abbreviations: SL, standard length; Pec L, length of longest pectoral ray; H max, greatest body depth; H min, least body depth; Width max, greatest body width; Sn, snout; OD₁, origin of the first dorsal fin; OD₂, origin of the second dorsal fin; OV, origin of ventral fins; TV, tips of ventral fins; OA, origin of anal fin; TA, last ray insertion of anal fin. Position of the fins and anus is expressed as a number of scales in front of (F) or behind (B) the point of reference.

	Holotype	Mean, range and standard deviation for holotype and 29 paratypes*	
	27.0 mm SL	17.9-29.6 mm SL	
In SL			
Head	3.2	3.3 (3.2-3.5)	.08
Pec L	4.3	4.6 (4.3-5.0)	.16
H max	3.8	4.2 (3.8-4.5)	.19
H min	9.5	9.6 (8.8-10.8)	.42
Width max	6.2	6.4 (6.1-6.7)	.17
Sn-OD ₁	1.8	1.8 (1.7-1.9)	.06
Sn-OD ₂	1.4	1.4 (1.4-1.5)	.02
Sn-OV ₂	2.1	2.2 (2.0-2.2)	.06
Sn-TV	1.5	1.7 (1.5-1.7)	.06
Sn-OA	1.6	1.6 (1.5-1.6)	.03
Sn-TA	1.2	1.2 (1.2-1.3)	.03
In head			
Eye	2.8	2.7 (2.5-2.9)	.11
Interorbital	2.5	2.6 (2.4-2.9)	.11
Postorbital	2.5	2.6 (2.3-2.8)	.14
Caudal peduncle length	1.8	1.7 (1.5-1.9)	.13
In eye			
Snout	1.8	1.7 (1.5-2.0)	.16
Premaxilla	1.4	1.5 (1.3-1.8)	.15
Premaxillary process	4.1	4.3 (3.2-5.6)	.63
Scale counts			
Midlateral scales	29	29 (28-30)	.61
Transverse scales	6	5.4 (5-6)	.24
Pedorsal scales	11	12.1 (11-13)	.43
Interdorsal scales	5	4.1 (4-5)	.5
Cleithrum-OV	5	6.7 (5-7)	.62
Fin elements			
First dorsal spines	5	4.8 (3-5)	.51
Second dorsal rays	7	7.0 (6-8)	.49
Anal rays	11	11.5 (11-13)	.63
Pectoral rays	11	10.7 (10-11)	.46
Position of fins			
OD ₁ to TV	F2	F2.1 (F1-3)	.63
OD ₁ to T Pec	—	B2.0 (B1-3)	.62
OD ₂ to Anal	B4	B3.1 (B2-4)	.64
OV to T Pec	—	F2.7 (F2-4)	.57
Other values			
Gill rakers in first lower gill arch	16	16.8 (16-18)	.65
Position of anus to TV	F5	F3.5 (F3-5)	.62
Vertebrae	30	30.2 (29-31)	.58

*Unless otherwise indicated. Numbers in bracket preceding mean, indicates the number of specimens counted or measured (some specimens are damaged).

External morphology

Relatively small, laterally compressed species, known specimens not exceeding 30 mm SL. Mouth small but unrestricted by labial ligament. Premaxilla with strongly curved, villiform teeth on its free border, extending almost as far as its distal end. Ramus of premaxilla broad with short median process and small rounded lateral process (Fig. 2c). Free edge of premaxilla with distinct concavity in anterior half with dentary recessing into it. Maxilla slender. Posterior ramus of lower jaw highly elevated. Teeth on dentary smaller than on premaxilla, curved, villiform and restricted to first third or half of lower jaw. Both jaws oblique to horizontal and not extending as far as vertical through anterior border of eye. Teeth present on palatines, ectopterygoids, vomer and basihyal in some specimens. Pelvic girdle attached to rib of 6th vertebra. Principal caudal rays always 8+7. Sexual dimorphism not apparent. Lateral body scales moderately large, cycloid, crenulate, dorsoventrally elongated, with circuli prominent on anterior half of scale only. 3 to 4 scales on preopercle and one large and several smaller scales on opercle. Large circular scale over interorbital space followed by larger semi-circular scale and rest of predorsal series. Ventral axillary scale large and distinct. Unpaired fins short when compared with other species of *Pseudomugil*. First dorsal not reaching origin of second dorsal. Third ray longest in second dorsal fin. Ventrals not reaching origin of anal. Anal fin spine always present. Pectoral fins pointed. Caudal moderately forked. Gill rakers numerous, moderately long and slender but less than half diameter of pupil.

Colour

Preserved specimens yellow green. Eye black. Dorsum of head dark, with concentration of melanophores on snout and postorbital part of head. Rim of lower half of eye outlined by melanophores. Side of snout, chin and opercle heavily peppered with small and large melanophores. Narrow but well defined black middorsal band originating on dorsum of head and extending through bases of dorsal fins to origin of caudal. Scale pockets on side of body well outlined by melanophores. Some melanophores also scattered within perimeter of each scale pocket with greatest concentrations of these in pockets of midlateral scale row. Midlateral band narrow dark line at its origin at dorsal base of pectoral, and continuing as two narrow lines from above origin of anal to caudal fin. Concentrations of melanophores on each scale along side of body forming faint discontinuous streaks, about four in number, excluding midlateral stripe. Bases of fins outlined by pigment; dark thin line through middle of scales directly above base of anal. Extremities of second dorsal and anal fins peppered with fine melanophores. Spines of first dorsal and rays of pectoral outlined by pigmentation. Body apparently translucent in life and with posterior end of swimbladder clearly visible even in preserved specimens, terminating ventrally at origin of anal and dorsally below vertebral column about 2 scales behind vertical through origin of anal.

Etymology

Helodes (Greek), meaning marshy. Like several other species of *Pseudomugil*, the new species occurs in mangrove swamps or in marshy habitat.

NEW SPECIES OF *PSEUDOMUGIL*

TABLE 2. Diagnostic attributes of 8 species of *Pseudomugil*. Ranges incorporate data from literature as indicated. The means were obtained from the specimens examined in this study except for *P. signifer*. Abbreviations: as in Table 1.

	<i>P. inconspicuus</i>	<i>P. novaeguineae</i>	<i>P. paludicola</i>	<i>P. gertrudae</i>	<i>P. helodes</i>	<i>P. majusculus</i>	<i>P. signifer</i>	<i>P. tenellus</i>
In SL Head H min	3.8(3.6-4.2) 10.0(9.2-11.0)	4.3(4.0-4.5)* 11.1(9.6-12.3)	3.7(3.5-4.2)* 7.4(6.7-8.0)	3.5(3.3-3.9)* 7.9(7.5-8.1)	3.3(3.2-3.5) 9.6(8.8-10.8)	3.8 10.1	3.8(3.4-4.3)* 9.4(8.3-11.6)	3.4(3.3-3.6) 9.1(8.5-9.6)
In Head Interorbital Postorbital	2.8(2.5-3.0) 2.6(2.3-3.0)	2.6(2.4-2.7) 2.7(2.4-2.9)	2.2(1.9-2.5)* 2.4(2.2-2.5)	2.1(2.0-2.3) 2.2(2.0-2.4)	2.6(2.4-2.9) 2.6(2.3-2.8)	2.1 2.7	2.3(1.9-2.5) 2.6(2.3-2.8)	2.7(2.5-2.8) 2.4(2.3-2.9)
In eye Premaxillary process	2.0(1.8-2.4)	2.6(2.2-3.4)		2.7(2.4-3.4)	4.3(3.2-5.6)	2.7	2.9(2.3-3.6)	3.8(3.2-5.1)
Scale counts Transverse Predorsal	5.0(5-6) 16(14-17)	6-7* 17(14-18)*	5 15.3(13-16)	6.4(6-7) 12.4(10-13)*	5.4(5-6) 12.1(11-13)	5 12	5.7(5-6) 11.5(10-12)	7.9(7-9) 12.0(11-14)
Fin elements Anal rays Pectoral rays	10.0(9-11) 10.2(10-12)*	10.4(9-12) 10.8(10-13)*	11.4(10-14)* 10.5(10-13)*	9.2(8-10) 8.8(7-11)*	11.5(11-13) 10.7(10-11)	12 10	10.4(9-12)* 9.3(8-13)*	7.1(6-9) 10.0(9-11)
Position of fins OD ₁ to TV OD ₁ to TPec	B2.5(1-3.5) B4.9(3-6.5)	B2.6(2-3) B6	B2.8(2-4) B5.4(4-7)	F5.3(2.5-2.8) B1.6(B3-F2)	F2.1(1-3) B2(1-3)	F3 B3	F3.7(2.5-5) B0.9(0-3)	F2.5(1-4) B2.2(1-4)
Other values and Attributes Gill rakers in first lower gill arch Vertebrae Spine in anal fin	11.3(10-12) 29.8(29-31) present	8.3(8-9) 33(31-35) present	8.6(8-10) 27.8(27-30)* present	10(9-11) 28.9(28-30) present	16.8(16-18) 30.2(29-31) present	14 28 ?	10.3(9-12) 28.6(27-29) absent	9(8-10) 27.8(26-28) absent

* means and ranges based on
Hadfield's *et al.* raw data (1979)

* ranges
incorporate
Roberts' (1978)
Allen and
Moore's (1978)
data
(1967) data

RELATIONSHIP TO OTHER SPECIES OF *Pseudomugil*

It appears that the genus *Pseudomugil* is composed of two distinct groups:

1. *P. inconspicuus*, *P. novaeguineae* and *P. paludicola* have high predorsal scale counts (Table 2). The first dorsal fin originates far back along the body, slightly in front of vertical through the origin of anal in *P. novaeguineae* and behind that vertical in the other two species.
2. *P. tenellus*, *P. gertrudae*, *P. signifer* and *P. belodes* all have their dorsal fins in a more anterior position as had already been noted by Allen and Moore (1981) for the first three.

P. belodes can be readily distinguished from the other members of the second group: from *P. gertrudae* it is distinguished by the coloration, the anal ray fin count and the more slender caudal peduncle in *P. gertrudae*. From *P. tenellus* it can be distinguished by the vertebral, gill raker, anal fin ray and the transverse scale row counts. *P. belodes* is most closely related to *P. signifer* but is easily distinguished from the latter by its high gill raker count, the crenulation of the body scales as well as by the presence of a spine in the anal fin in *P. belodes* but not in *P. signifer*. Although a number of meristics as well as morphometric measurements of the two species overlap, their means are distinct and different for the prepectoral fin count, position of first dorsal fin, length of premaxillary process, width of interorbital space and length of head.

DISTRIBUTION

The present known distribution of *P. belodes* is restricted to islands just north west and west of New Guinea. This is the westernmost known extreme of the range for the species of the family Melanotaeniidae. The species appears to inhabit mangrove swamps. Since other species of *Pseudomugil* (e.g. *P. signifer*) are known to inhabit a variety of habitats, from freshwater streams to bays and estuaries with high salinities, it is not unlikely that *P. belodes* may also be found in other habitats.

PSEUDOMUGIL MAJUSCULUS, NEW SPECIES

Pseudomugil species "B" Allen and Cross, 1982: 130.

Holotype — USNM 236542, 31.9 mm SL, rotenone in 1 m of water, in mangroves, Cape Ward Hunt, Papua New Guinea, 08° 04.2'N 148° 08.4'E, 17 June, 1979, collected by Bruce B. Collette, "Alpha Helix" Expedition, 1979. The description is based on the holotype, the only known specimen of the new species.

GENERAL DESCRIPTION

Meristics and Morphometrics

All of the measurements and counts taken are presented in Table 3.

External morphology

One of larger species of *Pseudomugil* (others usually less than 30 mm SL) with moderately compressed body. Mouth small but unrestricted by labial ligament.

NEW SPECIES OF *PSEUDOMUGIL*

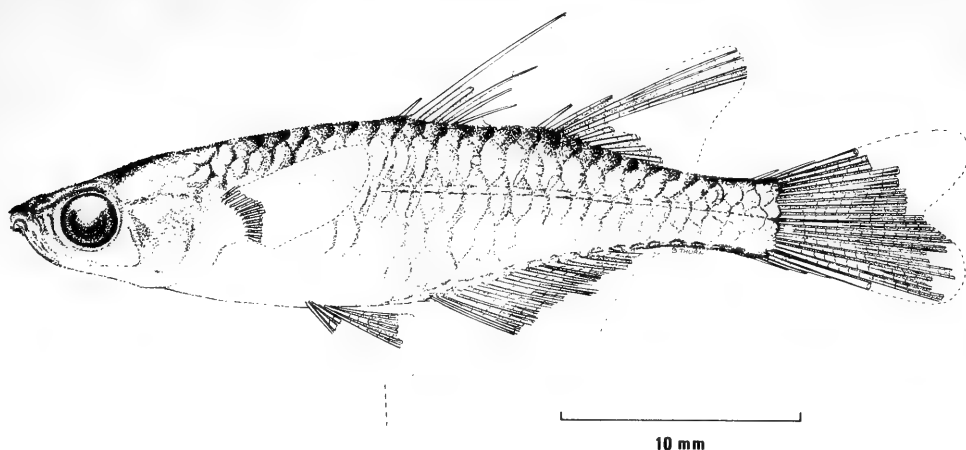


Fig. 3. *Pseudomugil majusculus*, line drawing of the holotype USNM 236542, 31.9 mm SL.

TABLE 3. Measurements and counts made on the holotype of *Pseudomugil majusculus*. Abbreviations: as in Table 1.

SL	31.9	Scale counts	
In SL		Midlateral scales	26
Head	3.8	Transverse scales	5
H max	4.1	Predorsal scales	12
H min	10.1	Interdorsal scales	4
Width max	6.6		
Sn-OD ₁	1.9	Fin elements	
Sn-OD ₂	1.4	First dorsal spines	5
Sn-OV ₂	2.3	Second dorsal rays	7
Sn-TV	1.7	Anal rays	12
Sn-OA	1.7	Pectoral	damaged, about 10
Sn-TA	1.3		
In head			
Eye	2.7	Position of fins	
Interorbital	2.1	OD ₁ to TV	F3
Postorbital	2.7	OD ₂ to Anal	B3
Caudal peduncle length	1.3		
In Eye		Other values	
Snout	1.7	Gill rakers in first lower gill arch	14
Premaxilla	1.4	Position of anus to TV	F3
Premaxillary process	2.7	Vertebrae	28

Premaxilla broad with short median process and with no lateral process (Fig. 2a), with its free border notched anteriorly. Teeth on free border of premaxilla in several rows near symphysis and with another two teeth midway along its free edge (Fig. 2a). Dentary with strong villiform teeth pointing backwards and extending at least half way along dentary. Posterior of dentary elevated. Teeth

not apparent on other bones except for mesopterygoids. Pelvic girdle attached to rib of 6th vertebra. Principal caudal rays 8+7. Holotype probably male (not dissected) since second spine of first dorsal extended into filament as in males of *P. signifer*. Second and third rays of second dorsal also long. Body scales large, cycloid, dorsoventrally elongated, with indistinct circuli restricted to anterior half of scale. Posterior edge of scale entire. Gill rakers short, less than half diameter of pupil but not tubercular in shape.

Colour

Preserved specimen yellow green. Eye black. Dorsum of head dark with concentration of melanophores on top of snout and preorbital part of head. Melanophores fine and less numerous on side of snout, chin, preopercle and opercle. Discontinuous middorsal band originating on dorsum of head, extending through dorsal fins and terminating at origin of caudal. Scale pockets outlined by very fine melanophores with some melanophores also scattered within perimeter of each scale pocket. Midlateral band restricted to narrow line originating from about 6th scale behind dorsal origin of pectoral to about hypural joint. Faint, discontinuous streaky line directly above midlateral line and two other less prominent lines above it. Bases of fins slightly darker than surrounding areas. Elements of dorsal fins pigmented; those of anal to lesser degree. Edges of rays in caudal pigmented. Body probably translucent in life.

Etymology

Majusculus (Latin), meaning somewhat larger or greater, thus implying that this species grows to a larger size than other species of *Pseudomugil*.

Remarks

Although the holotype of *P. majusculus* is in relatively good condition, all of its fins are damaged to a greater or lesser degree. There are good indications that in life, the dorsal and the ventral fins were extended into filaments and the former were strongly pigmented. It is difficult to assess whether the first element of the second dorsal and anal fins are spines or unbranched rays. The scales in this species are quite deciduous and are absent from some parts of the head and the anterior lower half of the body. For this reason the cheek scales and those between the cleithrum and the origin of ventrals were not counted.

RELATIONSHIP TO OTHER SPECIES OF *Pseudomugil*

Pseudomugil majusculus can be distinguished from *P. inconspicuus*, *P. novae-guineae* and *P. paludicola* by a low predorsal scale count and the more anterior position of the origin of the first dorsal fin; from *P. gertrudae*, by the coloration of the latter and the anal fin ray count; from *P. tenellus*, by the gill raker, anal fin ray and transverse scale row counts; from *P. belodes*, by the gill raker count and the absence of crenulation of scales in *P. majusculus*; and from *P. signifer*, by the gill raker count and the gill raker length.

NEW SPECIES OF *PSEUDOMUGIL*

In the genus *Pseudomugil*, the shape of the premaxillary bone appears to be diagnostic at the specific level (see Roberts, 1978 and Fig. 2). However, the shape of the premaxillaries of *P. majusculus* and *P. signifer* is very much alike and of no diagnostic value. On the other hand, the length of the gill rakers and their greater number in *P. majusculus* are regarded as specialised characters. None of the large sample of *P. signifer*, taken from its entire range, from fresh, estuarine and saline waters and examined by Hadfield et al. (1979) had moderately elongate and slender gill rakers or with their number exceeding 12 in the first lower gill arch.

On the basis of the characters examined (Table 2), *P. majusculus* appears to be closest to *P. signifer* but is distinct from it as discussed above.

DISTRIBUTION

So far, only one specimen has been collected from the northern coast of New Guinea, near Cape Ward Hunt. It appears likely that the species may be restricted to a small geographic area since there have been numerous collections made both on the north and the south coast of New Guinea in recent years.

ACKNOWLEDGEMENTS

We would like to thank Dr Bruce B. Collette for collecting and sending us specimens of the new species. We are also grateful to Miss Betty Thorn, Macquarie University artist, for her line drawings.

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The Reproductive Biology of Summer Whiting, *Sillago ciliata* C. & V., in Northern Moreton Bay, Queensland

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ABSTRACT

Monthly samples of summer whiting (*Sillago ciliata*) occurring at Bribie Island were taken from August, 1980 to July, 1981. Seven stages of gonadal maturity could be identified in male fish and eight in females. One stage, that of spent fish, was not observed in either sex. The prolonged spawning season extended from September to March. Ova diameter analyses indicated that females have the potential to spawn at least twice during the spawning season. Male *S. ciliata* significantly ($P < 0.05$) outnumbered female fish (1.3:1.0). *S. ciliata* larger than 24 cm fork length were predominantly female, whereas smaller fish were predominantly male. The fecundity of individuals measuring 21-31 cm fork length ranged from 31,000 to 380,000 eggs. The relationship between fecundity (Y) and fork length (F.L.) was:

$$Y = -299,764 + 17,695 (\text{F.L.})$$

INTRODUCTION

Summer whiting, *Sillago ciliata* Cuvier and Valenciennes, 1829 (Order Perciformes Family Sillaginidae) occur along the east coast of Australia from northern Tasmania (40°S) to Townsville (19°S). They are commonly found over shallow (< 10 m) sandy bottom, particularly off surf beaches and in estuarine areas. The species is of significant economic importance in New South Wales and Queensland where large quantities are taken by recreational and commercial (tunnel-net or beach seine) (Anon 1982) fishermen. The present study area, Bribie Island in northern Moreton Bay (27°S), is a major fishing area for summer whiting in Queensland. The fishery appears to be associated with aggregations of *S. ciliata* during the spawning period. In spite of the economic importance of summer whiting, little is known of the reproductive characteristics of this species and no information is available from the Bribie Island area.

Tosh (1903) and Munro (1945) have described the eggs and larvae of *S. ciliata* collected in southern Queensland. Limited information on growth, feeding,

reproduction and habitat requirements of this species is given by Cleland (1947) for New South Wales and Queensland, and by Dredge (1976) for southern Moreton Bay. Spawning seasons and reproductive behaviour of other Sillaginidae have been described by Ogilby (1893), Roughley (1916), Scott (1954), Prabhu

TABLE 1. Distinctive features of the gonads of *S. ciliata* at different stages of maturation.

Maturity Stage	Macroscopic characteristics	Microscopic characteristics
Testes		
I Immature virgins	Testes appear as a thin black-grey strip.	Lobules poorly defined. Spermatogonia predominate.
II Immature	Grey to black, broad and flattened in cross-section. Extend $< \frac{1}{4}$ way into body cavity from urogenital opening.	Lobules clearly defined, mainly primary and secondary spermatocytes.
III Developing virgins, resting adults	Grey, triangular in cross-section, extend $< \frac{1}{2}$ way into body cavity from urogenital opening.	Primary and secondary spermatocytes predominate although many spermatids present.
IV Maturing	Grey, occupy $\frac{1}{2}$ - $\frac{3}{4}$ of abdominal cavity.	Spermatids and spermatozoa predominate.
V Ripe	Whitish, occupy $\frac{3}{4}$ of abdominal cavity, milt extruded by abdominal pressure.	Spermatozoa predominate.
VI Running-ripe	Whitish, fill abdominal cavity giving the fish a swollen appearance, milt extruded by abdominal pressure.	Lobules gorged with spermatozoa.
VII Spent	Not observed.	Not observed.
Ovaries		
I Immature virgins	Ovaries appear as a thin translucent strip, sex difficult to determine without histological techniques.	Type A* and B oocytes, mostly type A. Ovary wall thin (17.6-49 μm) often folded.
II Immature	Translucent to pale yellow, cylindrical in cross-section, individual ova not visible.	Type A and B, mostly type B. Ovarian wall variable in thickness (28.6-114.4 μm) but not folded.
III Developing virgins, resting adults	Pale yellow, small whitish ova visible, gonads extend $< \frac{1}{2}$ into body cavity from urogenital opening.	Type A, B and a few small type C oocytes. Ovarian wall 28.6-157 μm .
IV Maturing	Bright yellow, oocytes clearly visible, ovary fills $\frac{3}{4}$ of abdominal cavity.	Type A-D, type D up to 472 μm . Types A-C form distinct clusters between Type D. Ovarian wall 64.4-128.7 μm .
V Ripe	Yellow, ovary fills almost all of abdominal cavity, giving the fish a swollen appearance.	All types present, type D and E predominate.
VI Running-ripe	Pale yellow with translucent areas, ovary fills abdominal cavity, ova extruded by abdominal pressure.	All types present, type E predominate. Ovarian wall 28.6-64.4 μm .
VII Partially-spent	Ovary flaccid, pink, small yellow oocytes visible, extend $\frac{3}{4}$ way into body cavity from urogenital opening yet body cavity appears shrunken externally.	Types A-D, septa arranged loosely with conspicuous spaces. Type C and D do not press tightly together as in Stage IV-VI.
VIII Spent	Not observed.	Not observed.

*Type A: Densely staining cytoplasm, several nucleoli, polygonal in outline, $< 35 \mu\text{m}$ in diameter. B: Peripheral nucleoli, chromatin threads clearly visible in nucleus, 49-98 μm . C: Yolk vesicles and small oil globules scattered throughout cytoplasm, 94-300 μm . D: All parts of cytoplasm contain yolk vesicles, fewer but larger oil globules than in Type C, radial striations in zona radiata, 300-580 μm . E: Mature, 580-688 μm , single oil globule 157-179 μm , collapse during histological processing. (Classification after Htun-Han 1978).

REPRODUCTIVE BIOLOGY OF SUMMER WHITING

(1956), Radhakrishnan (1957), Palekar and Bal (1960), Caton (1966) and Maclean (1969). The present study investigates the reproductive biology of *S. ciliata* at Bribie Island, and describes spawning frequency and season, fecundity and variation in sex ratios.

METHODS

Specimens of *S. ciliata* were collected during 12 consecutive months (August 1980 to July 1981) from sand banks off southern Bribie Island (27°00'S, 153°10'E). Fish were collected on two occasions each month during the spring tides, using a 150 m beach seine (2.5 cm mesh). The Fork Length (F.L.) of captured fish was measured to the nearest 0.5 cm, the gonads were examined macroscopically and allocated a maturity stage (Table 1). Fish less than 14 cm F.L. were not routinely examined as preliminary investigations revealed such fish were immature.

TABLE 2
Number of *S. ciliata* histologically examined at each maturity stage.

	Maturity stage							Total
	1	2	3	4	5	6	7	
Female	6	9	11	13	7	4	4	54
Male	7	5	6	9	3	3	—	33

To verify the stages of gonad maturity identified from macroscopic features randomly selected fish at each maturity stage were taken from monthly catches made during September — May (Table 2). Gonads were removed and fixed in Bouin's fluid (Luna 1968) for at least 48 hours in preparation for histological study. Transverse sections (5-9 μ m) were cut from the middle of each gonad and stained in Mayers haematoxylin and eosin. Ten to twenty oocytes at each stage of development (Table 1) were randomly selected from each ovarian section and the diameters measured to the nearest 1 μ m. Only oocytes which had been sectioned through the nucleus were measured. Terminology used to describe testes and ovaries is respectively that of Hyder (1969) and Treasurer and Holliday (1981).

Stage IV and V ovaries were removed from 39 fish (21-31 cm F.L.) captured in October and November and preserved in Gilson's fluid for use in fecundity studies. Ovaries from each fish were weighed (\pm 0.001 g) and a sample consisting of a transverse cross-section (1-5% of total ovary weight), which included the ovarian wall, was taken from the middle region of each ovary. Samples were weighed (\pm 0.0005 g) on filter paper, and carefully teased until separation of eggs was complete. An estimate of fecundity was obtained by counting the number of yolked eggs present in both samples and multiplying by the ratio of total ovarian weight/weight of samples. Fecundity would be overestimated if large numbers of ova were resorbed. All histological sections were therefore examined for evidence of resorption of ova.

Monthly samples of 5-10 female fish (Stages IV-VI: 19.5-32 cm F.L.) were randomly selected from collections made during September-March for use in ova size-frequency studies. Ovaries were removed and preserved in Gilson's fluid. A standard procedure of taking a random sample of ova from the middle region of the ovary was adopted and the diameters of 200-300 yolked ($>$ 0.13 mm diameter) ova from each sample were measured to the nearest 0.002 mm. Large numbers of small ($<$ 0.13 mm in

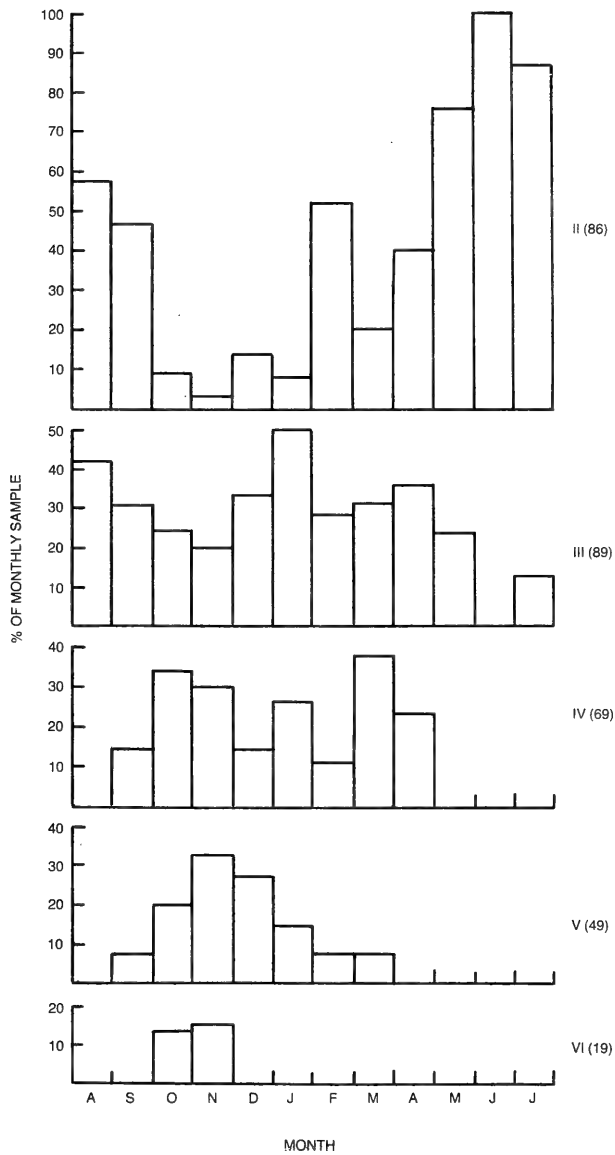


Fig. 1. Monthly percentage of male *S. ciliata* at Stages II-VI. Data for Stage I (immature virgin) individuals were not included. Number of specimens is shown in parentheses.

REPRODUCTIVE BIOLOGY OF SUMMER WHITING

diameter) unyolked ova were present in all ovaries but were not included in the present analysis. The frequency of ova diameter measurements from each ovary was expressed as a percentage of the total ova counted for that ovary and plotted on a size frequency graph. Separation of modes was attempted using probability paper methods proposed by Harding (1949) and Cassie (1934). These methods while indicating polymodality do not indicate the magnitude of modes involved and often the modes indicated by such methods consisted of extremely few ova. In the present context such minor modes (< 5% of total ova counted) were regarded as being biologically insignificant and were not considered further. The major size groups of ova were readily separable in terms of diameter and external appearance and did not require statistical definition.

RESULTS

Examination of *S. ciliata* gonads revealed that the ovaries could be placed in eight maturity stages and the testes in seven. Spent gonads were not observed. Each stage may be defined by characteristic macroscopic and microscopic features (Table 1). Individuals at stages V and VI of maturity (♀:19-32 cm F.L.; ♂:17.5-30 cm F.L.) were captured from September to March (Figs 1 and 2). Partially-spent (Stage VII) female *S. ciliata* were observed in October and November indicating that spawning had occurred recently. Gonads from all fish sampled from May to August were either immature or resting (Stages I-III).

The overall female to male ratio for fish larger than 14 cm F.L. was 1.0:1.3 ($P < 0.05$, Chi-square). Sex ratios differed significantly ($P < 0.05$) from the expected 1:1 ratio in September and November, 1980 and January and April, 1981 (Table 3). Males significantly ($P < 0.05$) outnumbered females in size classes less than 24 cm F.L. and females significantly ($P < 0.05$) outnumbered males in larger size classes (Fig. 3).

TABLE 3

Sex ratio for monthly samples (August 1980 - July 1981) of *S. ciliata* (>14 cm F. L.) from Bribie Island. A chi-square test was used to test for difference between the observed sex ratio and the expected 1:1 ratio.

MONTH	SAMPLE SIZE	♀ : ♂
August	18	1:2.0
September	48	1:0.4*
October	125	1:1.1
November	102	1:1.8*
December	22	1:2.1
January	63	1:1.7*
February	39	1:1.1
March	29	1:0.8
April	31	1:2.4*
May	29	1:1.4
June	18	1:1.0
July	23	1:1.9
TOTAL	547	1:1.3*

* = significant at $p < .05$

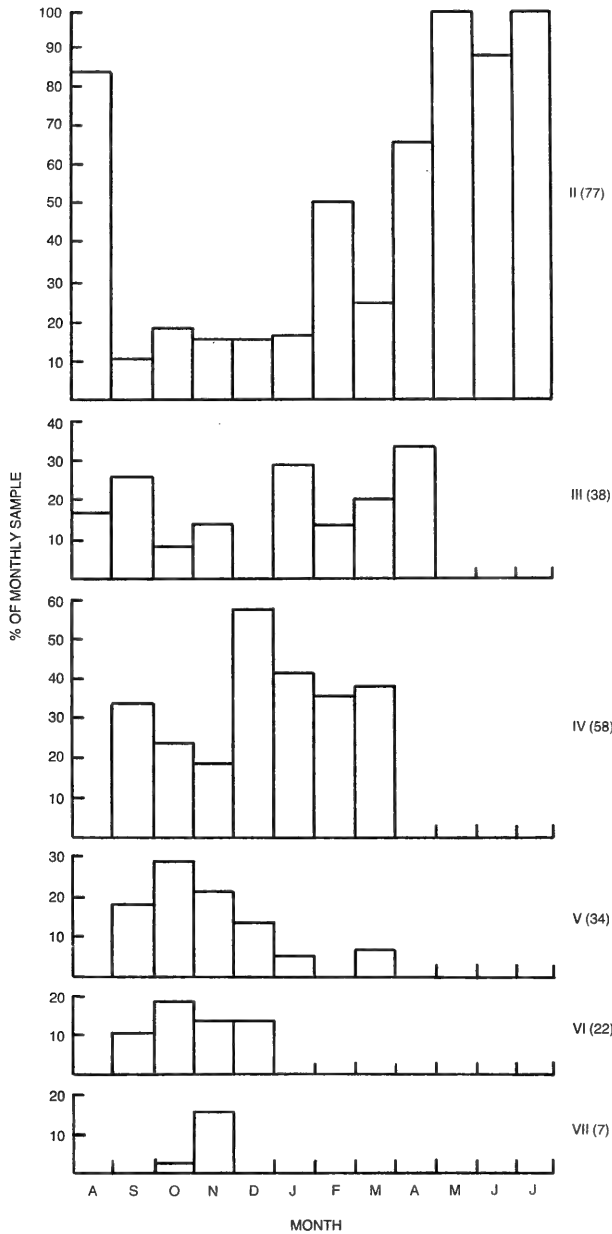


Fig. 2. Monthly percentage of female *S. ciliata* at Stages II-VII of maturity. Data for Stage I (immature virgin) individuals were not included. Number of specimens is shown in parentheses.

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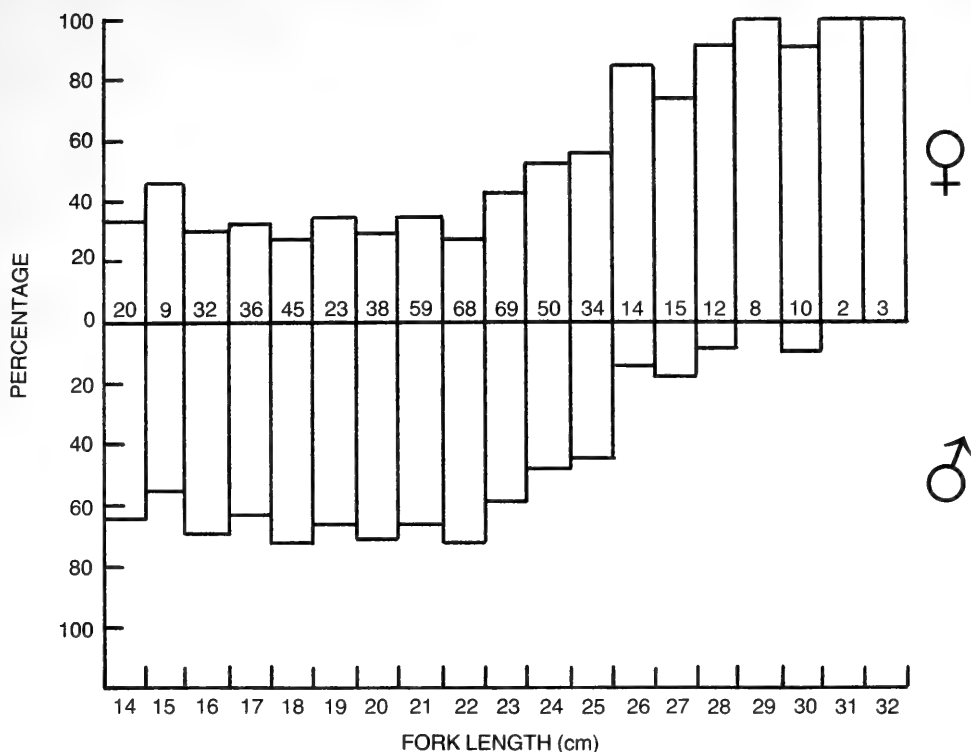


Fig. 3. Sex ratio (%) of *S. ciliata* 14 cm (F.L.) and larger. Number of specimens is shown at 0% line.

Estimates of fecundity ranged from 31,000 to 380,000 ova (mean \pm S.E. = $147,372 \pm 11,449$, $n = 39$). Resorption of ova was recorded in only one of the 54 ovaries histologically examined. These degenerating oocytes accounted for only 5.1% of the maturing (Types C and D, Table 1) oocytes present in the ovary (stage VII) and thus correction for oocyte resorption was not made when estimating fecundity. The regression equation and correlation coefficient for the relationship (Fig. 4) between fecundity and fork length is:

$$\text{Fecundity} = -299,764 + 17,695 (\text{F.L.}) \quad r = 0.63$$

(F.L. — fork length, cm)

In September (the first month of the spawning season) all ova-diameter frequency polygons derived from ovaries were bimodal (e.g. Fig. 5a). At this time of the year Stage VI ovaries contained two modes of yolked ova, one maturing (mode y), the other mature (mode x) (Fig. 5a). Mature ova were semi-transparent (0.58 mm–0.69 mm in diameter), contained a single oil globule

(0.16 mm–0.18 mm in diameter), and were readily separated by diameter from the partially yolked maturing ova (0.30 mm–0.40 mm). Many ovaries from fish taken after September contained only a single size-class of yolked ova (Fig. 5b). The occurrence of fish with ovaries having two modes of yolked ova decreased during the spawning season (Fig. 6); conversely the proportion having one mode of yolked ova increased.

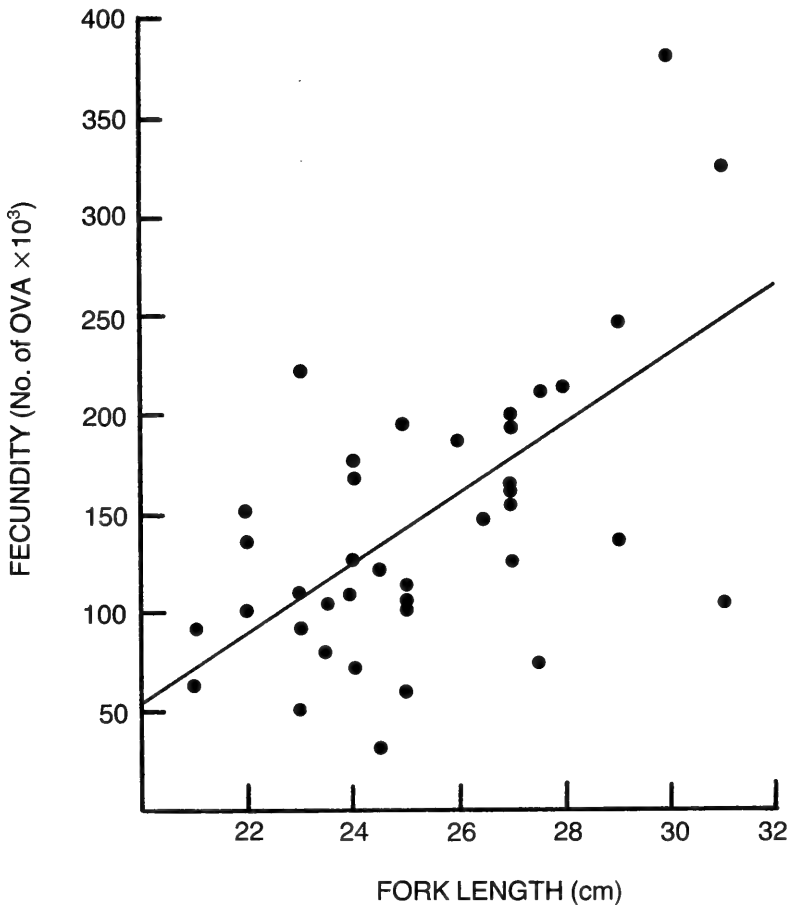


Fig. 4. Relationship between fecundity and fork length for 39 *S. ciliata* individuals at Bribie Island, October - November, 1980.

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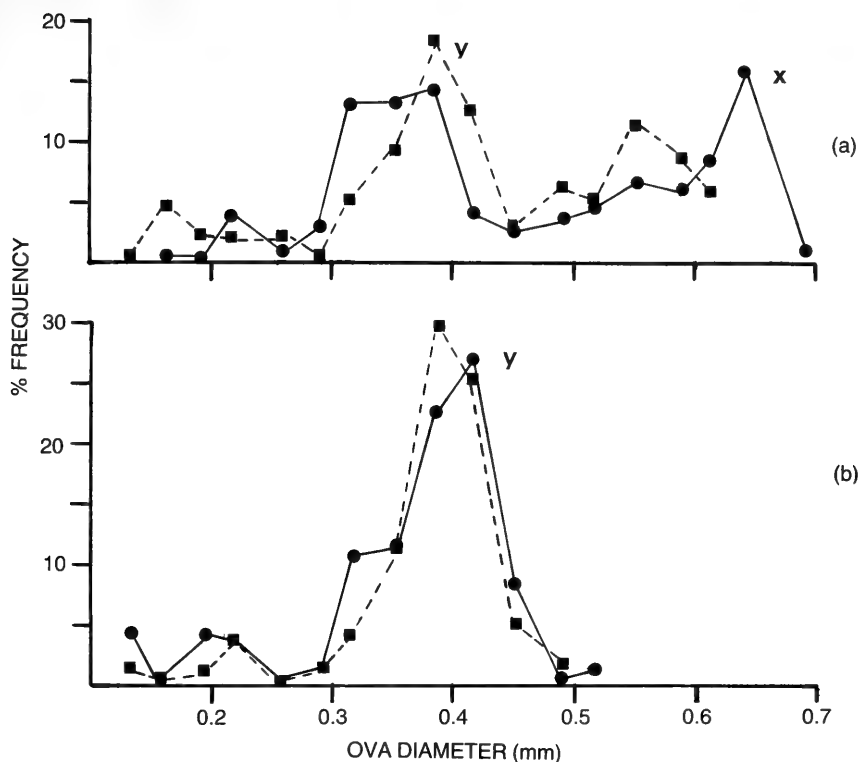


Fig. 5. Randomly selected examples of ova-diameter frequency polygons for yolked ova in a) Stage VI ovaries taken in September 1980 and b) Stage V ovaries taken in November 1980. Two specimens are shown in each graph. Major modes are indicated by x and y.

DISCUSSION

The spawning season of *S. ciliata* at Bribie Island extended from September to March as ripe or running-ripe fish were captured only during this period. A similar result was recorded by Dredge (1976) at Southport Broadwater, in that ripe or running-ripe *S. ciliata* were observed from September to February. Spent gonads were not observed. Presumably spent fish either migrated from the sampling area and/or the spent gonad condition exists for only a very short time period.

The observed change in sex ratios with increasing fish length (females being larger than males) could result from females growing faster than males and/or males suffering a higher mortality but no data are available to determine this. A similar change in sex ratios with size has been noted for *S. sihama* by Radhakrishnan (1957) and by Maclean (1969) for *S. maculata*. No evidence of sex reversal has been reported for the Sillaginidae.

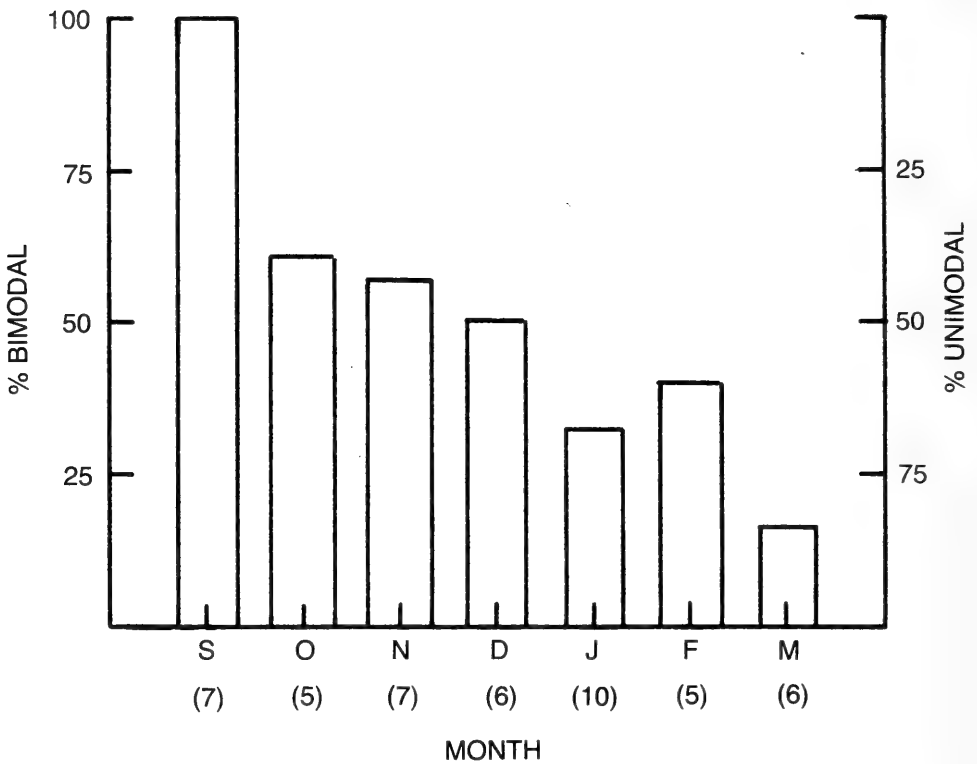


Fig. 6. Monthly occurrence (%) of bimodal and unimodal ova-diameter frequency polygons for Stage IV-VI ovaries. Number of specimens is shown in parentheses.

No previous estimate of fecundity for *S. ciliata* has been published. The wide range in fecundity estimates for fish of a given length (Fig. 4), may be due to environmental conditions such as food availability (Ware 1977) and/or multiple spawnings (see below). Maclean (1969) noted a wide range in fecundity (141,000 to 362,000) for a related species, *S. maculata*, which is a multiple spawner. Oocyte resorption was observed in only one specimen, the gonads of which were partially-spent (stage VII). Only type C and D oocytes (Table 1) appeared to be resorbed. The process of resorption in this single specimen appeared to be similar to that described in other oviparous fish by Gokhale (1957) and Treasurer and Holliday (1981).

The presence of different size groups of yolked ova in a fish ovary often indicates multiple spawnings (Dharmamba 1969, Le Clus 1979). As two prominent size groups of yolked ova were commonly observed in *S. ciliata* ovaries, it is

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likely that female *S. ciliata* are able to spawn at least twice within a single spawning season. Cleland (1947) also observed two size groups of yolked ova in ovaries of *S. ciliata* sampled in Sydney which he termed eggs of the first and second spawning. The single size group of yolked ova commonly observed in ovaries from fish sampled late in the spawning season could occur when the larger (in terms of diameter) size group of ova seen in bimodal polygons (Fig. 5a: mode x) has been spawned and the smaller size group of ova (Fig. 5a: mode y) continues to mature. The spawning season lasted for seven months (September-March) and therefore there should be sufficient time for more than one batch of ova to develop to maturity. *S. ciliata* at Bribie Island did not seem synchronized in the time of spawning, as the ovaries from fish taken during the spawning season contained either one or two major size groups of yolked ova (Fig. 6).

The strategy of reproductive output being spread over an extended time period may confer certain advantages. Summer whiting, like many coastal species (e.g. *Acanthopagrus australis*, *S. maculata*), spend part of their juvenile life in mangrove areas or seagrass beds (Munro 1945). The prolonged spawning season may reduce intra- and inter-specific competition (e.g. for food or space) between juveniles in these habitats. Spawning over an extended time period may also result in a reduction of the impact of adverse environmental conditions on larval or juvenile survival.

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The Tolerance to Fluoroacetate of Geographically Separated Populations of the Quokka (*Setonix brachyurus*)

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ABSTRACT

The tolerance to fluoroacetate of three geographically separated populations of the macropodid marsupial, the quokka (*Setonix brachyurus*) in southwestern Australia is compared in terms of elevation of plasma citrate levels in response to dosing with 1080.

The populations from mainland Western Australia and from Bald Island off the south coast of W.A. are currently in contact with fluoroacetate-bearing plants. These populations have a much higher tolerance to fluoroacetate and are more genetically homogeneous for the resistance than the population on Rottnest Island off the west coast of Western Australia. The latter population has been isolated from contact with fluoroacetate-bearing vegetation from some 5,000-7,000 years, but is much more tolerant than are macropodids in southeastern Australia where fluoroacetate-containing plants are not known to occur.

INTRODUCTION

The compound sodium fluoroacetate (1080), commonly used as a vertebrate pesticide, occurs naturally in 34 species of the legume genera *Gastrolobium* and *Oxylobium*, 33 of which are confined to southwestern Australia (Aplin 1971). The evolution of genetic tolerance to fluoroacetate in species of mammals exposed to this substance in nature has recently been demonstrated (Oliver et al. 1977; King et al. 1978) and some of the biochemical aspects of its detoxification have been elucidated (Mead et al. 1979). This acquired tolerance has been used as a genetic marker in studies to trace past radiations of these species (Oliver et al. 1979) and has emphasized the value of 1080 in Western Australia as a target specific pesticide for the control of sensitive exotic predators such as the fox (*Vulpes vulpes*) (King et al. 1981). Information on the susceptibility of native fauna to the toxin is essential in order to minimise the risk from pest control programs to non-target species. Fox, feral cat and rabbit control is carried out in areas of Western Australia for the purpose of conservation of a number of species of small to medium-sized native mammals.

This paper compares the tolerance to fluoroacetate of geographically separated populations of the quokka (*Setonix brachyurus*) from mainland Western Australia where toxic species of *Gastrolobium* and *Oxylobium* are wide-spread; from Bald Island, Western Australia where *Gastrolobium bilobum* (heart-leaf poison) is common and from Rottnest Island, Western Australia where fluoroacetate-bearing vegetation does not occur.

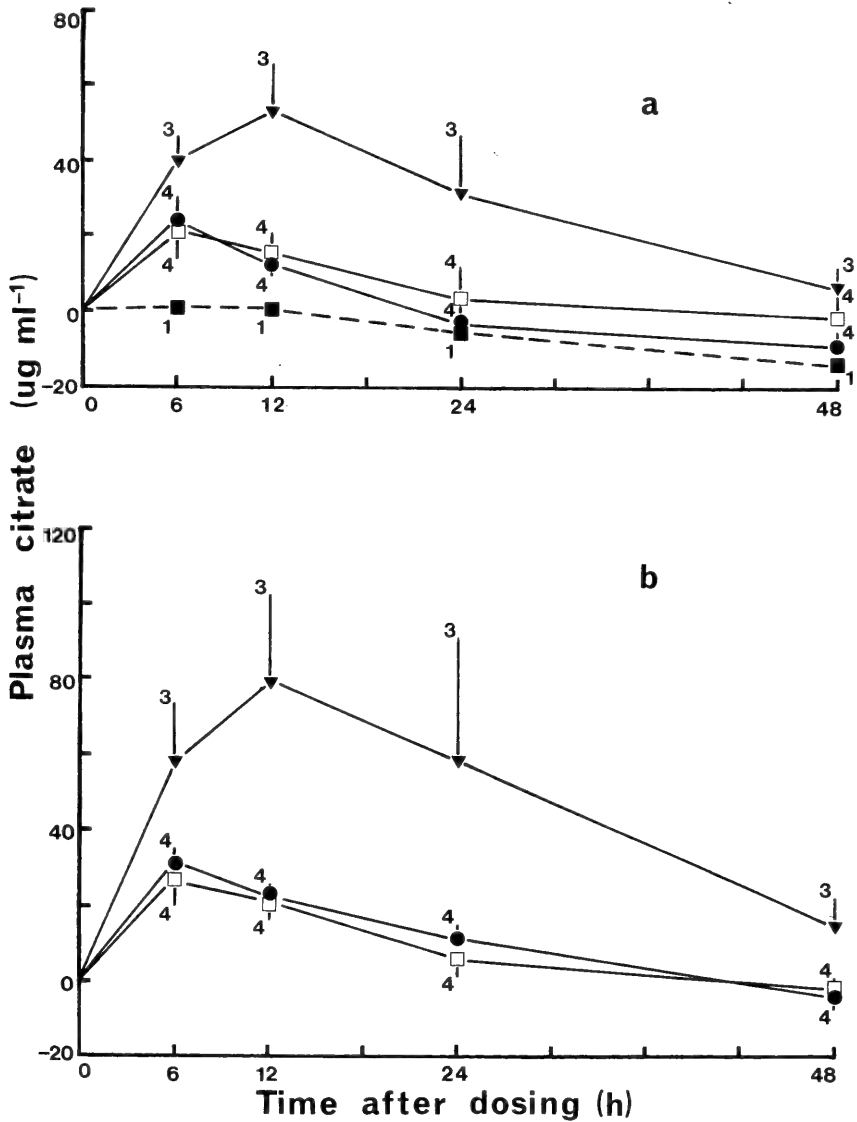


Fig. 1. Mean and Standard Error of the increase above base-level (time zero) values of plasma citrate concentrations following intraperitoneal administration of (a) 3.0 mg 1080 kg⁻¹, (b) 5.0 mg 1080 kg⁻¹, to the Quokka. Symbols: ▼ Rottnest Island, ● Bald Island, □ Mainland Western Australia, ■ Undosed Mainland Western Australia. Numbers beside the symbols represent the number of animals.

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MATERIAL AND METHODS

ANIMALS:

Adult *Setonix brachyurus* were collected in the field from localities near Pemberton and Dwellingup on the Western Australian mainland, from Bald Island near Albany, Western Australia, and from Rottnest Island, near Fremantle, Western Australia. Animals were held individually in rabbit cages in animal houses at 22°C and 70% relative humidity and maintained on a 12:12 hour photoperiod. Animals were provided with commercial kangaroo food pellets (Milnes Stock Feeds, W.A.), apples and cabbages. Water was provided ad libitum.

DOSING:

Animals were dosed intraperitoneally with aqueous solutions of commercial grade 1080 (94% sodium monofluoroacetate by HPLC analysis) obtained from Rentokil Laboratories Ltd.

BLOOD SAMPLING:

Blood samples for the determination of plasma citrate levels were collected from the lateral caudal vein using heparinized syringes and scalp-vein sets, after warming the tail with hot water to facilitate venipuncturing. Samples were immediately centrifuged and the plasmas frozen and stored at -20°C while awaiting analysis.

CITRATE DETERMINATION:

As in our previous studies, plasma citrate concentration was determined by the method of Camp and Farmer (1967).

STATISTICAL ANALYSIS:

The elevation in plasma citrate concentration displayed by the three quokka populations after intraperitoneal administration of various doses of 1080 was analysed statistically. To assess significant differences between the three populations within each dose level, a single factor analysis of variance (Keppel 1973) was carried out on the 6 h and 12 h plasma citrate elevations. The Scheffé test was employed to test differences and the harmonic mean was used to compensate for uneven group sizes (Keppel 1973).

RESULTS

Increases in plasma citrate levels following dosing of *S. brachyurus* with various doses of 1080 are shown in Figs 1-3. The increases in plasma citrate concentration in the Rottnest Island population at 3 and 5 mg 1080 kg⁻¹ were significantly higher ($p < 0.05$) 12 hours post-dosing than those exhibited by the Bald Island and mainland populations (Fig. 1). The latter two populations did not differ significantly from each other at these dose levels at either the 6 or 12 hour bleeds ($p > 0.05$). Three of the six Rottnest Island animals administered 10 mg 1080 kg⁻¹, died, displaying large elevations in plasma citrate concentration, whereas all Bald Island and mainland quokkas survived doses of both 10 and 20 mg 1080 kg⁻¹ (Fig. 2). The latter two populations did not differ significantly from each other 6 or 12 hours post-dosing at either the 10 or 20 mg 1080 kg⁻¹ dose level ($p > 0.05$). One of the three mainland animals administered 40 mg 1080 kg⁻¹ died 24 hours post-dosing but all Bald Island animals survived (Fig. 3). Citrate accumulation patterns for both populations at this dose level were almost co-incident and did not significantly differ at either the 6 or 12 hour bleed

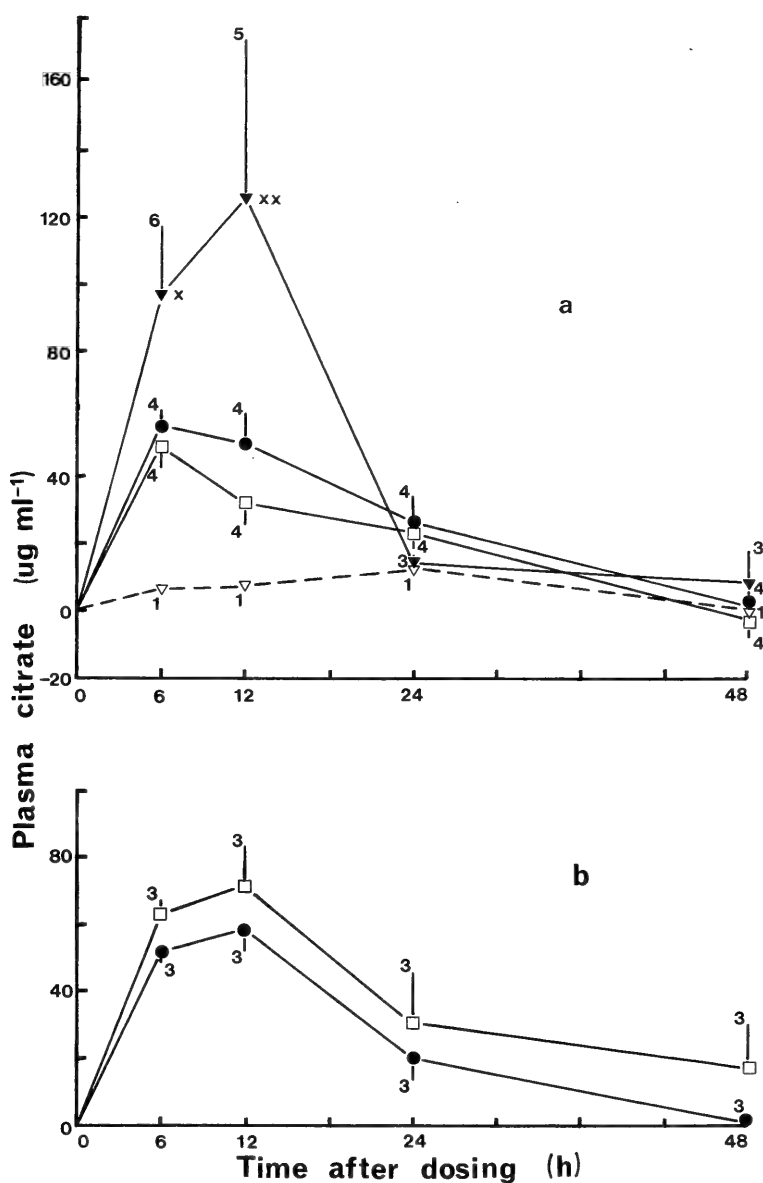


Fig. 2. Mean and Standard Error of the increase above base-level (time zero) values of plasma citrate concentrations following intraperitoneal administration of: (a) 10.0 mg 1080 kg⁻¹, (b) 20.0 mg 1080 kg⁻¹, to the Quokka. Symbols: ▼ Rottnest Island, ● Bald Island, □ Mainland Western Australia, ▽ Undosed Rottnest Island. Numbers beside the symbols represent the number of animals. X indicates death of animal.

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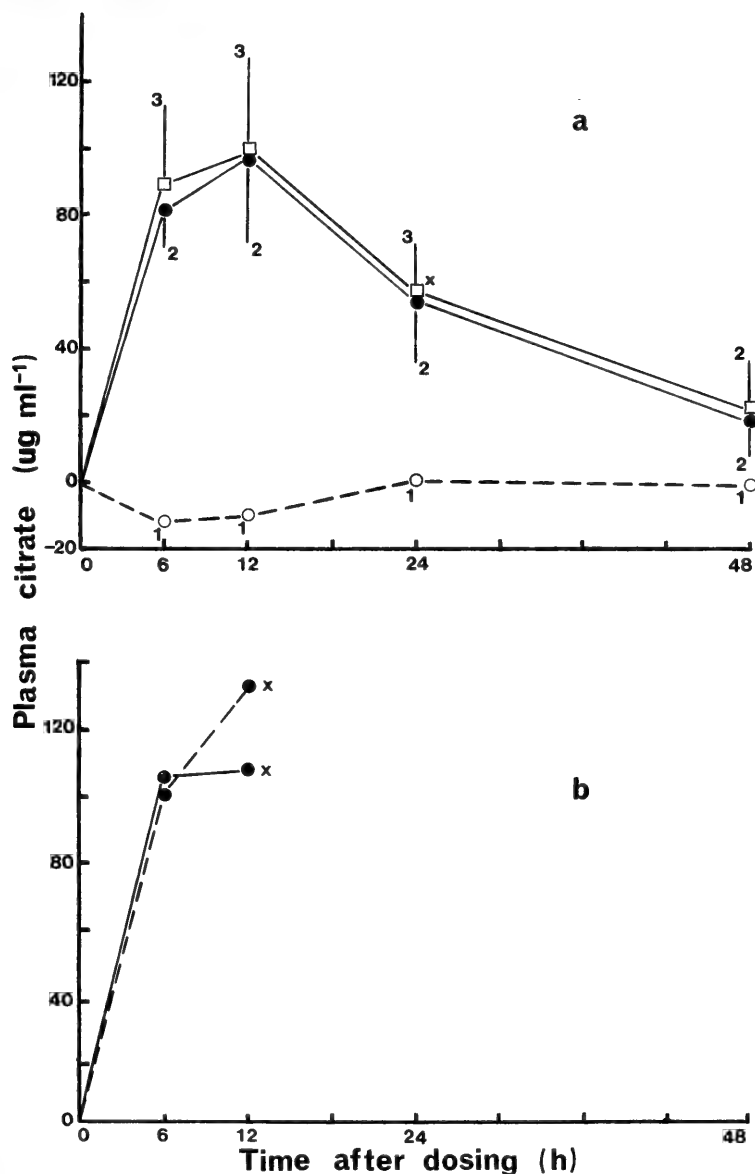


Fig. 3. Increase above base-level (time zero) values of plasma citrate concentrations following intraperitoneal administration of: (a) 40 mg 1080 kg⁻¹ (Mean and Standard Error), (b) 60 mg 1080 kg⁻¹ (individual animals are shown), to the Quokka. Symbols: ● Bald Island, □ Mainland Western Australia, ○ Undosed Bald Island. Numbers beside the symbols represent the number of animals. X indicates death of animal.

($p > 0.05$). Both Bald Island animals administered 60 mg 1080 kg⁻¹ died 12 hours post-dosing showing rapid plasma citrate accumulation (Fig. 3).

The variation in citrate response in individual animals from each of the three populations dosed with 10 mg 1080 kg⁻¹ is shown in Fig. 4. The Rottneest Island population displayed more heterogeneity than either of the other populations. Three animals accumulated large amounts of citrate and died, one immediately after the 6 h bleed and two after the 12 h bleed, while the other three animals survived, showing a citrate response typical of the Bald Island and mainland populations (Fig. 4).

DISCUSSION

Elevation of plasma citrate levels in response to dosing has previously been shown to reflect the susceptibility to 1080 intoxication of animals with similar metabolic rates (King et al. 1978). This technique which is more ethically acceptable and more economical than LD₅₀ testing is therefore most applicable to the assessment of the tolerance or susceptibility to 1080 of separated populations of conspecifics or of closely related species (King et al. 1981).

The tolerance to 1080 of *S. brachyurus* is similar to that reported for some other endemic south-western Australian fauna (Oliver et al. 1977, 1979; King et al. 1978, 1981) and is substantially higher than that of eastern Australian macropods which have not had contact with fluoroacetate-bearing vegetation (McIlroy 1982). The high tolerance to 1080 of south-western Australian fauna appears to be the result of long-term association with food plants containing fluoroacetate. Though the dietary intake by the quokka of the toxic species of *Gastrolobium* and *Oxylobium* is unknown, another macropodid, the western grey kangaroo (*Macropus fuliginosus ocydromus*) has been shown to consume seven fluoroacetate-bearing species of *Gastrolobium* and *Oxylobium* at most times of the year (Mead 1980). It also appears that the grey kangaroo may have learnt to limit its intake of the most toxic species and to consume larger amounts of the least toxic thus achieving a balance between adequate nutrition and the avoidance of being poisoned (Mead et al. 1985).

The Bald Island and mainland populations of *S. brachyurus* appear to have a similar tolerance to 1080 with an LD₅₀ value apparently in the region of 40-60 mg 1080 kg⁻¹. Palaeontological studies have shown that *Setonix* was abundant in south-western W.A. at least 30,000 years BP (Merilees 1967, 1979; Balme et al. 1978). As it is probable that the capacity to produce fluoroacetate evolved once many thousands of years ago in a south-western form ancestral to the 34 present day fluoroacetate-bearing species of *Gastrolobium* and *Oxylobium*, it is likely that *Setonix* has been exposed to fluoroacetate for a long period of time. Bald Island became separated only 9,000 years ago (Main 1961) from a mainland region where heavy non-alkaline soils support the growth of toxic species of *Gastrolobium* and *Oxylobium* (Aplin 1971). One might expect that

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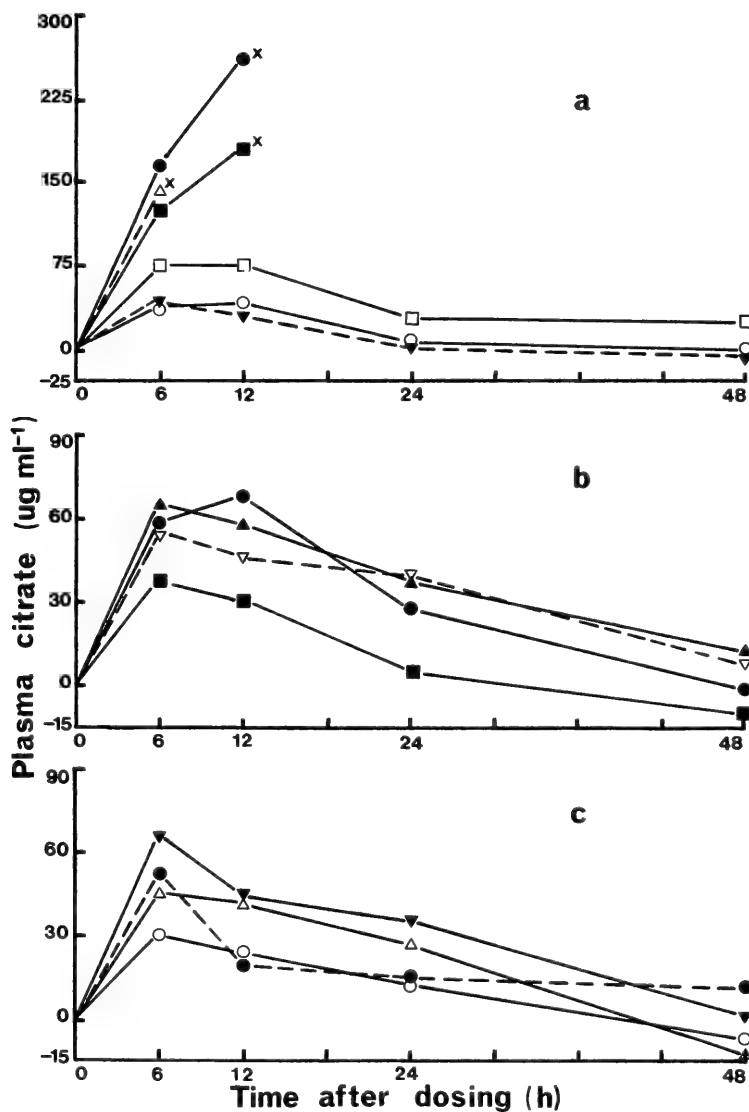


Fig. 4. The increase above base-level (time zero) values of plasma citrate concentrations for individual animals from three Quokka populations following intraperitoneal administration of $10 \text{ mg } 1080 \text{ kg}^{-1}$. (a) Rottnest Island, (b) Bald Island, (c) Mainland Western Australia. X indicates death of animal.

a population isolated on an island would be more frequently forced to rely on a particular food item than would a population on the mainland but the similarity in tolerance to fluoroacetate of the Bald Island and mainland populations suggests that the former population is no more reliant on the leaves of *Gastrolobium bilobum* than is the latter. Bald Island has a mild, moist climate and supports a relatively abundant and diverse flora (Abbott 1981). As the quokka is known to accept a wide range of dietary items (Storr 1964) it is conceivable that food choices on the Island are relatively plentiful even in summer and that extensive reliance on *G. bilobum* is not necessary.

All Rottnest quokkas dosed with 5 mg 1080 kg⁻¹ survived (Fig. 1). This suggests that the LD₅₀ value of 2 mg 1080 kg⁻¹ based on our pilot dosing of animals from Rottnest Island, and cited by McIlroy (1982) was an underestimate. Three out of six animals from the Rottnest Island population survived 10 mg 1080 kg⁻¹ suggesting that the LD₅₀ may be closer to this value (Fig. 2).

The quokka population on Rottnest Island has not been exposed to fluoroacetate-bearing vegetation since separation of the island from the mainland about 5-7,000 years ago (Churchill 1959; Main 1961) and is likely to be descended from a population occupying the currently adjacent mainland and the intervening land surface which is now submerged. The habitat suitable for quokkas in this region is unlikely to have been suitable for the establishment of the toxic species of *Gastrolobium* and *Oxylobium* due to the presence of deep sands and limestone soils (Aplin 1971). This previous coastal population may therefore have differed in tolerance from the predecessors of the more southerly population, exposed to fluoroacetate-bearing vegetation from which our mainland animals were derived and from which our Bald Island animals appear to have originated. It seems likely that the genetic composition of this coastal population would have been heterogeneous with respect to fluoroacetate tolerance for the reason previously suggested to explain the heterogeneity in coastal populations of *Rattus fuscipes* (Oliver *et al.* 1979): namely a population which has not been selected for tolerance to fluoroacetate receiving a genetic contribution from more tolerant inland populations. The current heterogeneity of the Rottnest Island population (Fig. 4) may therefore reflect this situation.

The tolerance to fluoroacetate of mainland and Bald Island quokkas is sufficiently high and homogeneous to allow 1080 to be used for the control of introduced pests with little risk to these quokka populations. The lower tolerance and greater heterogeneity of the Rottnest Island population would make such a control program more difficult to implement but appropriate choice of bait material and 1080 content could still allow pest control programs to be carried out successfully.

This example of coevolution between animals and toxic plants illustrates how naturally occurring resistance to the toxins can be used to improve target-specificity in control programs directed at introduced pest species and provides

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further evidence for the impact of fluoroacetate-bearing vegetation on the genetic composition of mammal populations in the south west of Western Australia.

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Relevance of Zoogeographical Transition to Conservation of Fauna: Amphibians and Reptiles in the South-western Slopes of New South Wales

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ABSTRACT

Frogs and reptiles were surveyed in twelve forests on the south-western slopes of New South Wales. The location and size of the forests determined their faunal composition. Riverine forests had fewest species of reptiles and frogs. The other forests divided into eastern, central and western zones on the basis of faunal composition, the change on an east-west gradient marking the transition from coastal and montane (Bassian) fauna to inland (Eyrean) fauna. More than 75% of the recorded species reach their geographic limits within the slopes. The transition lies in the centre of the region and the fauna there was depauperate. Western forests were also depauperate, containing only 50% of the Eyrean fauna known to occur in the region and less than 25% of species found 200 km further west. The forests of the region serve principally to maintain the range of species. Most are of sufficient size to conserve the majority of their component herpetofauna, the exceptions being small western forests (c. 300 ha) that are surrounded by agriculture.

INTRODUCTION

The concept of faunal subregions within the Australian continent was first advanced by Spencer (1896), who delineated a northern Torresian, a south-eastern Bassian and a central Eyrean zone, the demarcation between the Bassian and Eyrean zones being the Great Dividing Range. Keast (1959, 1962) noted that the Spencer scheme agrees "fairly well" with the general distribution of major groups of reptiles and that there is "about a 50 per cent changeover of species . . . between coastal Sydney and the Dubbo area on the western slopes and about 150 miles inland". Cogger and Heatwole (1981) likewise conclude that reptile distributions "generally uphold the traditional view of Australia's major biogeographic subregions" although the location of boundaries varies from family to family. For amphibians, Horton (1973) and Littlejohn (1981) accepted the separation of a coastal fauna and an inland fauna in south-eastern Australia. The precise location of the boundary has been analysed for the avifauna by Kikkawa

and Pearse (1969), who found the demarcation in south-eastern Australia consistently bisected the south-western slopes of New South Wales.

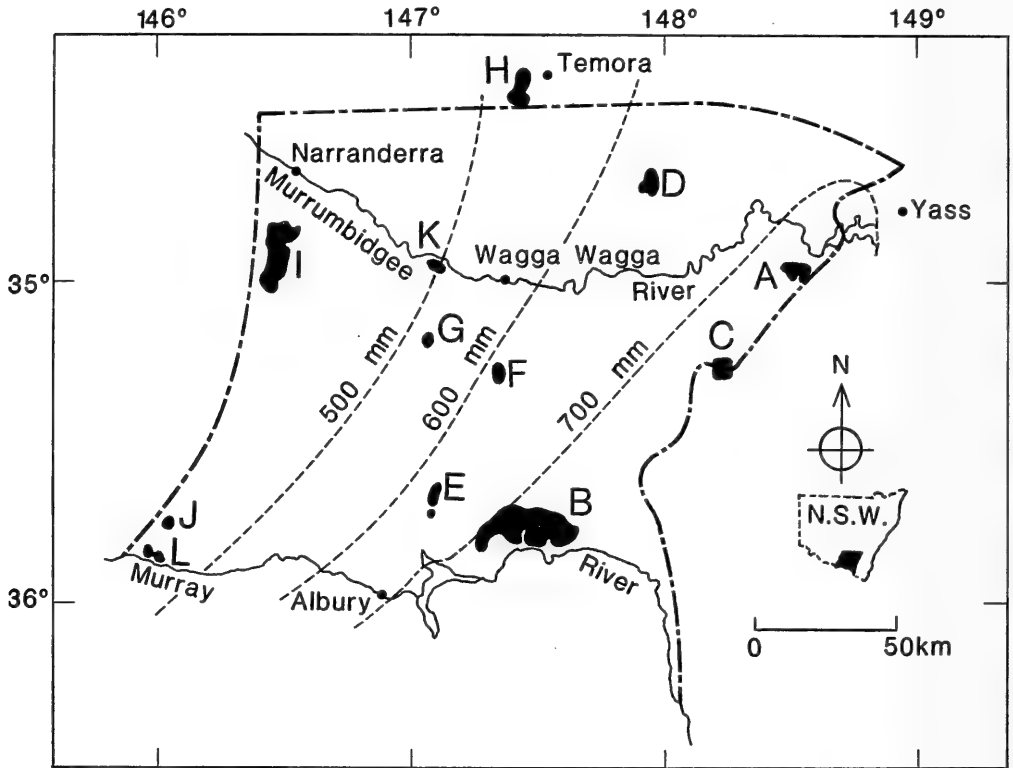


FIG. 1. Map of the south-western slopes of New South Wales showing the location of the areas surveyed, coded as in Table 1.

The south-western slopes (Fig. 1) is one of the biogeographical regions of New South Wales defined by Anderson (1968) and consistently used as the basis for representative conservation of flora. The boundaries of the regions are delineated principally by climate — for the south-western slopes, rainfall is between 400 and 900 mm per year falling predominantly in winter; winter frosts are common but snow is rare. Altitude varies from 600 m in the east (although some areas are as high as 1000 m) to 100 m in the west. Physiographically it comprises hilly, undulating and plains country.

Settlement of the region followed the expedition of Hume and Hovell in 1824, and by 1860 almost all the region was subdivided into pastoral holdings (Taylor 1959). Extensive clearing for wheat growing began soon after on the

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lower slopes. Typically the only land left uncleared was rocky hillsides and the higher slopes to the east where agriculture was restricted by the short growing season and high incidence of frosts. Today only 4 per cent of the region retains its original forest cover.

In this paper, we examine the effect of the zoogeographical boundary on the distribution of reptiles and amphibians in the south-western slopes of New South Wales and look at the relevance of the transition to the conservation of the herpetofauna in the region.

METHODS

Eleven forests representing a cross-section of the geographic and topographic variation in the south-western slopes, and Ingalba Nature Reserve just to the north, were surveyed (Fig. 1). The duration and times of survey are given in Table 1.

Reptiles were collected opportunistically. Most were caught by hand after sighting or searching under logs, rocks and bark. Some of the larger species were caught in Elliott traps set for small mammals. Frogs were found under logs and bark or by spotlighting around water at night, and tadpoles were collected and raised through to metamorphosis for identification. Specimens of most of the smaller species were taken and lodged in the Australian Museum. The taxonomy follows Cogger (1979).

TABLE 1. Summary of the survey of the southwestern slopes (S.F. = State Forest, N.P. = National Park, N.R. = Nature Reserve).

Code	Forest	Area (ha)	Month of survey	No. survey days	No. spp. frogs	No. spp. reptiles
A	Bungongo S.F.	2,000	Jun	7	8	6
			Jan	4	8	10
B	Dora Dora N.P.	33,000	Oct	7	6	13
	Proposal		Jan	9	8	11
C	Tumut S.F.	3,500	May	7	4	2
			Nov	2	5	9
D	Ulandra N.R.	3,000	Feb	4	5	8
			Nov	3	3	8
E	Tabletop N.R. and Benambra S.F.	1,500	Oct	8	2	10
			Oct	3	0	7
F	Livingstone S.F.	2,000	Mar	8	3	6
G	The Rock N.R.	300	Jun-Jul	7	0	5
			Jan	3	0	4
			Mar	1	3	—
H	Ingalba N.R.	3,500	Aug	10	0	5
			Feb	6	4	2
			Mar	2	—	6
I	Buckingbong S.F.	12,000	Apr	6	5	6
			Dec	6	6	10
J	Wahgunyah S.F.	300	Aug	4	1	5
K	Berry Jerry S.F.	1,200	Apr	2	0	1
			Dec	2	3	2
L	Boomanoomana and Mulwala S.F.'s	1,500	Aug	5	5	3

RESULTS

Species lists for the twelve areas are presented in Appendix Tables 1 and 2. In all, a total of 15 species of frogs and 37 species of reptiles were found*.

Before we compare the fauna of the different forests, the factors affecting the success of surveys require appraisal.

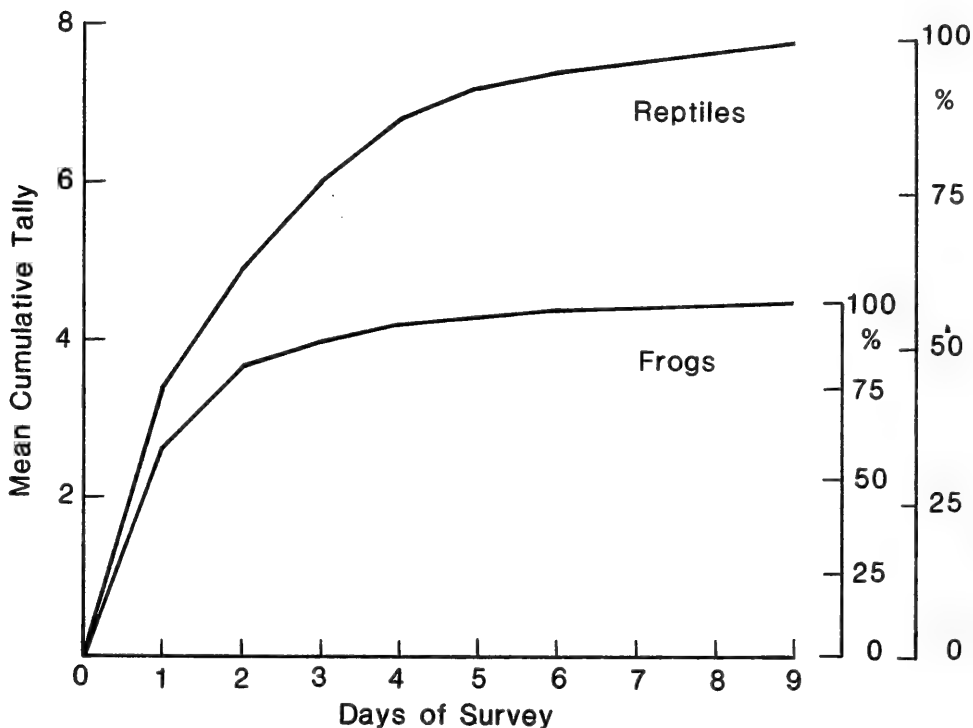


FIG. 2. Effect of effort on the number of species of frogs and reptiles found.

EFFECT OF EFFORT

The effect of effort was measured by plotting the number of days of survey against the cumulative total of species of frogs and reptiles averaged over all areas (Fig. 2). In eastern forests, frogs were found quickly and easily near water, and

* Confusion in distinguishing *Ranidella parinsignifera* from *R. signifera* through much of the survey has prevented accurate assessment of their respective distributions. Also, early collections of *Cryptoblepharus boutonii* were not identified to current taxonomic nomenclature.

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and the tally of species seldom increased after the second day. In western areas the rise was slightly slower because of the wider scattering of water bodies. Reptile tallies likewise accumulated rapidly. Approximately half of the total number recorded were found on the first day and 80% by 3.5 days. Thereafter the rate slowed markedly with continuing effort gradually turning up additional species.

Effort varied between the different forests, but few species would have been added if it had been equalised across all areas. For example, Wahgunyah was surveyed for only four days, but the relationship in Fig. 2 predicts that five more days of survey would have produced only 0.7 additional species of reptiles and 0.1 species of frogs.

EFFECT OF SEASON

There was no discernible effect of season on the number of species of frogs recorded (Fig. 3). Success depended on dampness of the ground and on standing free water rather than time of year. In contrast, the effect of season on reptile tallies was marked, with late spring the optimal time for survey (Fig. 3). A sinusoidal curve was fitted to the data by transforming the month of survey of $\cos t$, taking November as 0° (maximum) and May as 180° (minimum) (riverine areas were excluded because of their poor faunal tallies, each point lying well below those from other areas). The 'slope' of the regression, 2.7, differed significantly from zero ($t = 3.81$, d.f. = 16, $P < 0.01$).

The effect of season was mitigated by re-surveying many of the forests (Table 1) but three were visited only once (F, K, L). In these areas, time of survey accounts at least in part for the low number of species recorded. The curve suggests that had they been surveyed in November, an additional 2 to 4 species may have been found.

T. Annable (pers. comm.) has surveyed one of the forests (F) and found 3 species of reptiles — *Morethia boulengeri*, *Lerista bougainvillii* and *Diplo-dactylus vittatus* — that we did not record. To overcome the shortfall in our data due to time of survey, these species are included in the subsequent analyses. For the other two forests no additional data are available.

EFFECT OF FOREST SIZE

The number of species (S) of reptiles and frogs recorded in a forest increased with its area (A) in ha, such that $S = 1.8 A^{0.25}$ ($r^2 = 0.54$) (Fig. 4). The exponent 0.25 does not differ significantly from 0.30, the exponent predicted by the thesis that the number of species doubles with a ten-fold increase in area ($t = 0.64$, d.f. = 10) (Darlington 1957, MacArthur and Wilson 1967). Large forests generally had more species than smaller forests, irrespective of their location.

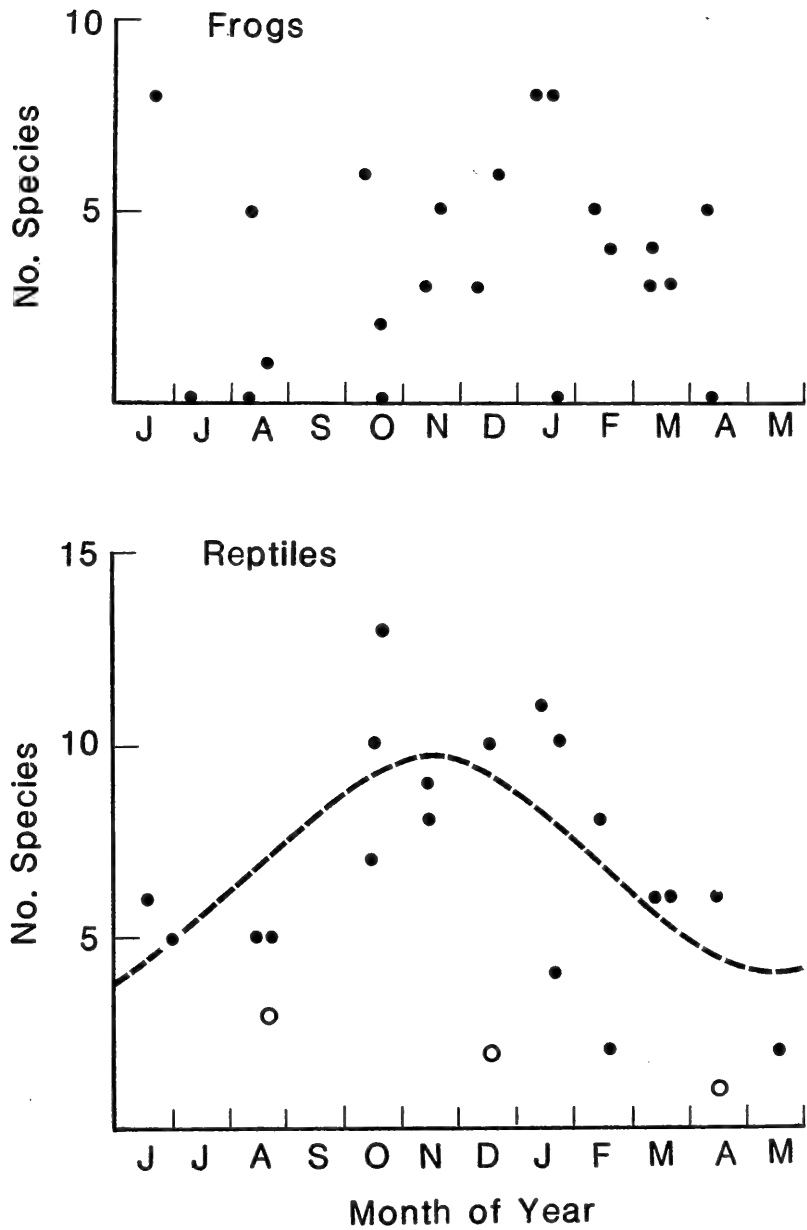


FIG. 3. Effect of season on the number of species of frogs and reptiles found (o = riverine forests).

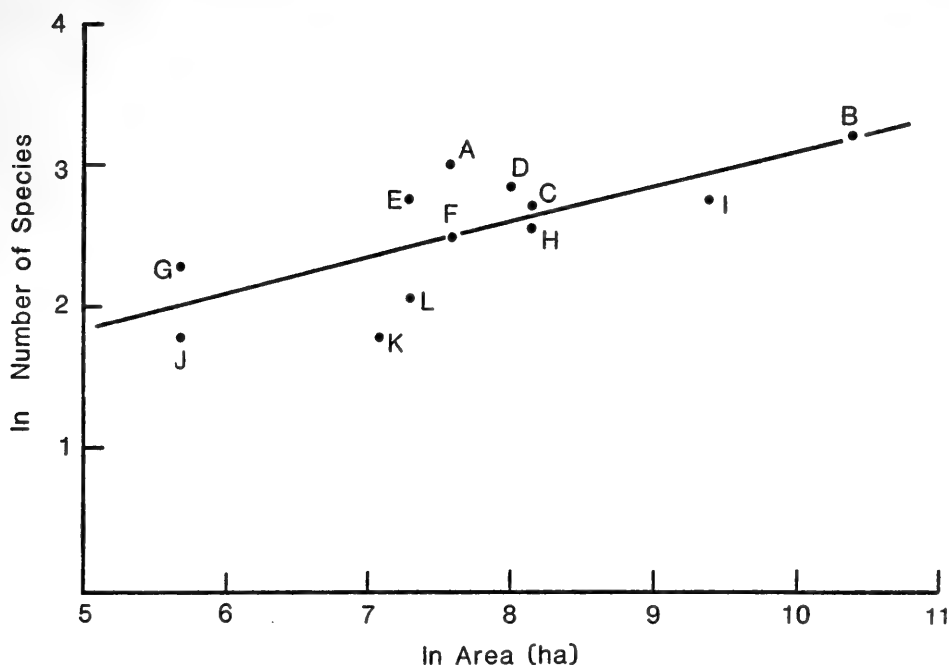


FIG. 4. Relationship between number of species of frogs and reptiles and size of forests, coded as in Table 1.

EFFECT OF HABITAT DIVERSITY

Although no quantitative assessment was made, most forests contained a variety of habitats. All had trees with loose bark, litter, fallen logs, shrubby areas and grassy areas, open glades and dense forest, although the extent of each varied from area to area. Both eastern and central forests were hilly to mountainous, with rock outcrops, sheltered gullies and dry ridges. Western areas were more undulating, reducing the diversity associated with slope and aspect. Rocky areas were absent but forestry practices of thinning and logging provided stumps with loose bark that substituted for rock crevices for some species (e.g. *Egernia striolata*). Eastern forests had moist habitats lacking in central and western areas. Water availability was good in the east where permanent creeks were present and the incidence of swampy areas was high. In the west, watercourses were impermanent and dams scattered through the forests for stock were the principal amphibian habitat. Riverine forests offered the least habitat diversity. Litter from the river red gums was sparse, the grassy understorey offered poor shelter and the loamy, cracking soil was unsuitable for burrowing species. On the basis of

habitat diversity, eastern forests could be expected to have the highest tally of species and riverine areas the lowest. These predictions are borne out in Fig. 4 where all the eastern forests (A to F) lie on or above the line of best fit, and the riverine and most of the western forests (G to L) below.

THE FAUNAL TRANSITION

Although the number of species recorded in a forest depended on its size and habitat diversity, the composition of the fauna varied with its location. For example, the ubiquitous *Lampropholis guichenoti* of the eastern forests was replaced by *Morethia boulengeri* in the west. A cluster analysis using Sorensen's index of similarity (Mueller-Dombois and Ellenberg 1974) was generated to explore the faunal disparity and the resulting dendrogram is shown in Fig. 5. The first separation (greatest dissimilarity) indicated the atypical nature of the riverine forests. The next fork separated out the western forests — Buckingbong, Wahgunyah, Ingalba and The Rock — from those to the east. There was only 43%

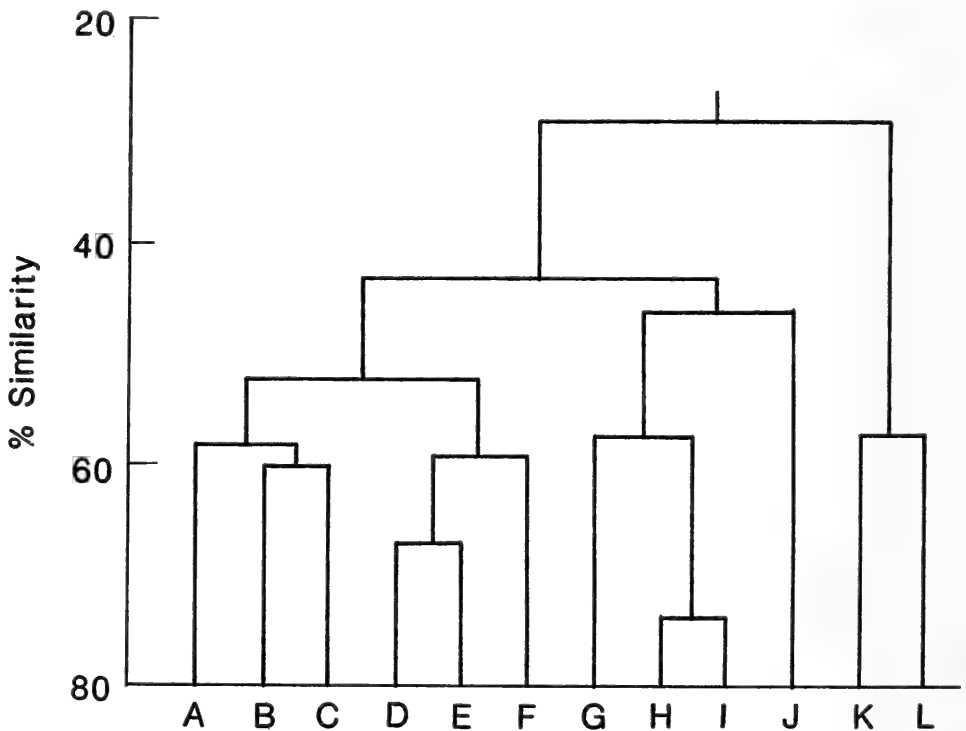


FIG. 5. Analysis of faunal similarity between forests on the south-western slopes, coded as in Table 1.

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similarity between the faunas of these groups of forests. The third fork separated the mountainous eastern forests adjacent to the tablelands from the rock outcrop forests in the centre of the region.

The faunal changeover between the east and west of the region is illustrated in Tables 2 and 3 where the species have been arranged according to their presence on an east-west gradient and to their classification as coastal or montane (Bassian), inland (Eyrean), or widespread species. The classifications were based on the distribution maps in Cogger (1979) — if the major part of a species' distribution was to the west of the region it was classed as Eyrean, if to the east, Bassian. In some cases the classification was difficult. Some species with primarily a Bassian distribution extended well into the Eyrean region (e.g. *Amphibolurus barbatus* *Pseudonaja textilis*). These were placed the 'widespread' category. Other species did not fall neatly into either zone (e.g. *Litoria raniformis*, *Carlia tetradactyla*) and their placement may be questionable. However, we hope that for the majority, the classifications are generally acceptable. There were no autochthonous species.

A sharp decline in eastern species and a gradual rise in western species is evident in these tables. The trends are graphed in Fig. 6 which illustrates the depauperate nature of both central and western forests, the central forests being particularly poor. Not only were there few species but those present were never as abundant as in similar habitats to the east and west. Hours of fruitless searching are a lingering memory of these areas.

TABLE 2. Appendix Table 1 reproduced with species of frogs classified as Bassian, Eyrean or widespread, showing (a) the decline in Bassian species as we progress westwards and (b) the low number of Eyrean species in western forests. Areas coded as in Table 1.

Species	A	B	C	D	E	F	G	H	I	J	K	L
BASSIAN												
<i>Uperoleia marmorata</i>	x											
<i>Litoria booroolongensis</i>	x	x										
<i>Limnodynastes peronii</i>	x	x										
<i>Litoria ewingii</i>		x										
<i>Limnodynastes dumerilii</i>	x	x	x									
<i>Litoria verreauxii</i>	x		x									
<i>Pseudophryne bibroni</i>	x	x	x	x	x							
WIDESPREAD												
<i>Ranidella</i> spp.	x	x	x	x	x	x	x	x	x		x	x
<i>Litoria peronii</i>	x	x	x	x		x		x	x		x	x
<i>Limnodynastes tasmaniensis</i>	x	x	x	x		x	x	x	x			x
EYREAN												
<i>Litoria raniformis</i>		x							x		x	x
<i>Limnodynastes interioris</i>				x			x	x	x			
<i>Uperoleia rugosa</i>									x	x		
<i>Limnodynastes fletcheri</i>												x

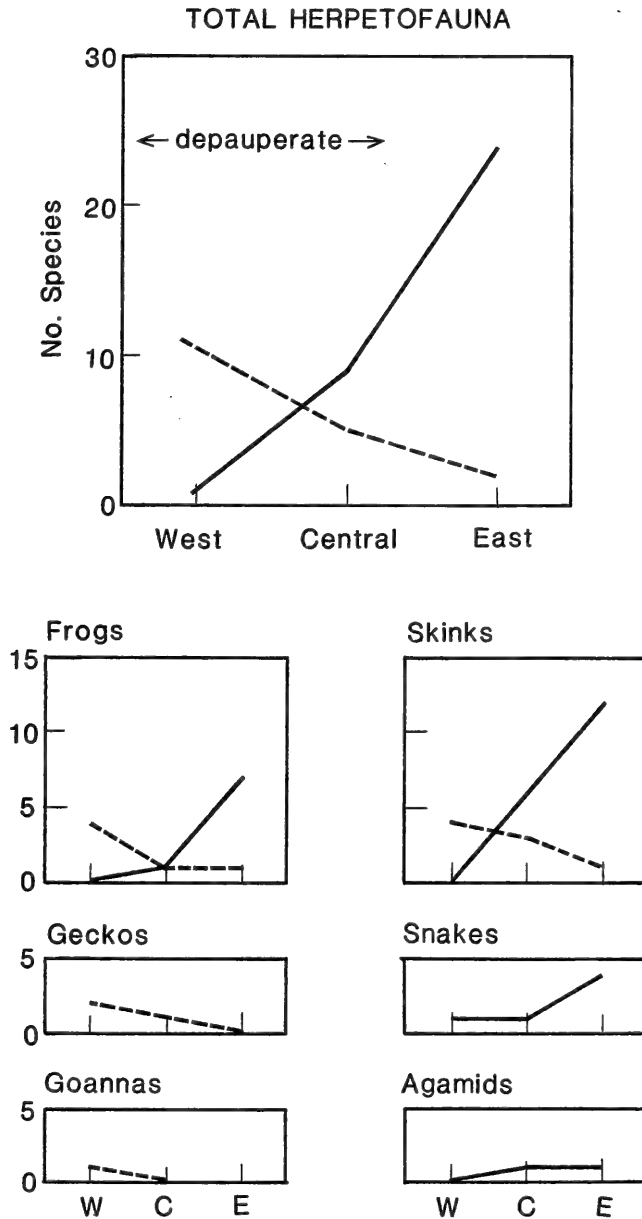


FIG. 6. Numbers of Bassian (—) and Eyrean (.....) species in eastern, central and western zones of the south-western slopes.

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The changeover was not uniform within the different groupings of herpetofauna (Fig. 6). Although frogs and skinks followed the transition described above, with Bassian and Eyrean faunas overlapping in the centre of the region, all geckos were either Eyrean or widespread species — no Bassian geckos were recorded. Conversely, all snakes and agamids were Bassian or widespread species. No Eyrean species were found in the forests surveyed.

TABLE 3. Appendix Table 2 reproduced with species of reptiles (excluding turtles) classified as Bassian, Eyrean or widespread, showing the decline in Bassian species and increase in Eyrean species from east to west. Areas coded as in Table 1.

Species	A	B	C	D	E	F	G	H	I	J	K	L
BASSIAN												
<i>Lampropholis delicata</i>	x											
<i>Leiopisma trilineata</i>	x											
<i>Egernia whitii</i>	x											
<i>Tiliqua nigrolutea</i>	x											
<i>Drysdalia coronoides</i>	x											
<i>Typhlina nigrescens</i>		x										
<i>Cryptophis nigrescens</i>		x										
<i>Hemiergis decresiensis</i>	x	x	x									
<i>Leiopisma platynota</i>		x	x									
<i>Sphenomorphus tympanum</i>	x	x	x	x								
<i>Egernia cunninghami</i>		x		x								
<i>Lampropholis guichenoti</i>	x	x	x	x	x							
<i>Lerista bougainvillii</i>		x				x						
<i>Amphibolurus muricatus</i>		x	x	x	x	x						
<i>Ctenotus taeniolatus</i>		x		x	x	x						
<i>Carlia tetradactyla</i>			x	x	x	x						
<i>Pseudechis porphyriacus</i>	x	x	x	x	x	x					x	x
WIDESPREAD												
<i>Varanus varius</i>		x	x	x	x	x	x	x	x			
<i>Pseudonaja textilis</i>		x			x			x	x	x		
<i>Amphibolurus barbatus</i>					x			x	x			
<i>Egernia striolata</i>	x	x		x	x			x				
<i>Diplodactylus vittatus</i>		x			x	x		x				
<i>Tiliqua scincoides</i>	x	x							x			
<i>Ctenotus robustus</i>					x							
<i>Demansia psammophis</i>					x							
<i>Lialis burtonis</i>							x					
EYREAN												
<i>Morethia boulengeri</i>			x	x	x	x	x	x	x	x		
<i>Trachydosaurus rugosus</i>				x								
<i>Phyllodactylus marmoratus</i>				x	x		x			x	x	
<i>Cryptoblepharus</i> sp./spp.						x	x	x	x	x		
<i>Diplodactylus intermedius</i>							x		x	x		
<i>Varanus gouldii</i>							x		x			
<i>Lerista muelleri</i>								x	x			
<i>Ctenotus strauchii</i>								x	x			

TABLE 4. Frogs and reptiles known to occur on the southwestern slopes but not found during the survey, classified as Bassian, Eyrean or widespread species.

Species	Bassian	Widespread	Eyrean	Source*
Frogs				
<i>Neobatrachus pictus</i>			x	A.M., A.N.W.C.
<i>Ranidella sloanei</i>			x	Littlejohn 1958
Reptiles				
<i>Gehyra variegata</i>			x	Annable
<i>Underwoodisaurus milii</i>		x		Annable
<i>Aprasia parapulchella</i>	x			Cogger 1979
<i>Delma impar</i>	x			Kluge 1974
<i>Delma inornata</i>			x	Kluge 1974, A.M., A.N.W.C., Annable
<i>Pygopus lepidopus</i>	x			Annable
<i>Pygopus nigriceps</i>			x	Kluge 1974
<i>Physignathus lesueurii</i>	x			Annable
<i>Menetia greyi</i>			x	Annable
<i>Typhlina australis</i>			x	A.M. (1892)
<i>Typhlina bituberculata</i>			x	Annable
<i>Typhlina proxima</i>			x	Annable
<i>Python spilotes</i>		x		Annable
<i>Austrelaps superbus</i>	x			Annable
<i>Furina diadema</i>		x		Annable
<i>Notechis scutatus</i>		x		Annable
<i>Unechis gouldii</i>			x	Annable
<i>Vermicella annulata</i>		x		A.M. (1889-94), Annable
No of species	5	5	10	

* Abbreviations in sources: A.M. — Australian Museum (date if last century); A.N.W.C. — Australian National Wildlife Collection.

Table 4 lists species not found during the surveys but known to occur in the region, based on the literature, museum collections and the personal collections of T. Annable. The species were classified as Bassian, Eyrean or widespread as before, and 50% were Eyrean forms. These Eyrean species could be absent from forests in the region, but it is perhaps more likely that the cryptic behaviour and low densities of some of the species (e.g. blind snakes, pygopodids) may indicate insufficient sampling rather than a real absence.

Even if these species are present, the western forests are still depauperate when compared with areas further inland. For example, the number of species is less than half that found in Round Hill Nature Reserve, 200 km to the north-west.

DISCUSSION

The prime attribute determining the species richness of a forest was its size, but because the slopes encompass a transition between Bassian and Syrean faunas, the species composition varied with location on an east-west gradient. Only 25%

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of the fauna were widespread species. The remaining 75% reach their geographic limits within the south-western slopes.

The boundary between the two major faunas closely approximates the demarcation noted by Kikkawa and Pearse (1969) for birds, but as found by Cogger and Heatwole (1981), the site of the transition differed between families of reptiles. Skinks, the most numerous group, matched the transition described above. Geckos were represented by Eyrean species only, suggesting the transition lies farther to the east for this group. These reptiles are principally Eyrean; true Bassian geckos are few. Agamids likewise have evolved primarily within the Eyrean zone, yet no Eyrean species were found in the slopes. Instead the family was represented there by "modified Bassian" species, and the transition zone for the group lies to the west. Cogger and Heatwole (1981) attribute these differences between families to differences in their patterns of adaptive radiations. The resultant is a broad zone of transition, and the fauna across the zone is markedly depauperate.

The transition is typical of the abutment of regional faunas — an 'overlapping of faunal elements, with progressive subtractions, in both directions' so that 'the transitional faunas are usually depauperate' (Darlington 1957). The reason for the transition is thought to be climate (e.g. Keast 1959). The eastern, central and western zones of the south-western slopes delimited by the 700 mm and 600 mm isohyets coincide with the divisions derived on the basis of faunal similarity of the forests (Fig. 1).

We have no estimates of the density or population size of any of the species in the forests. The number of sightings both within and between species varies according to their behaviour patterns and on ambient conditions. Very little is known of the home range requirements of Australian herpetofauna generally, but Turner *et al.* (1969) predict that small insectivorous lizards weighing 3 to 10 g will range over 0.05 ha to 0.15 ha. Frogs and small snakes may have ranges of the same order of magnitude. Small species therefore will reach high densities in a forest whose size is measured in thousands of hectares, provided habitat is well represented. In these circumstances, if a species was recorded in a forest, it is likely that its numbers are sufficient to represent that species' conservation there.

For larger species of reptiles, more care is required. The large skinks and agamids are omnivorous or totally herbivorous and have relatively small home ranges, comparable in size to those of smaller insectivorous reptiles. For example, the bearded dragon *Amphibolurus vitticeps* has a calculated home range of 1.8 ha (Badham 1971), less than half the 4.5 ha predicted by Turner *et al.*'s (1969) equation. Yet the large skinks and agamids were never common in forests. They appear to prefer open woodland where because the incidence of solar radiation is higher, they can reach activity temperatures more rapidly. They would therefore

not be disadvantaged in pastoral country, but the extensive clearing and agriculture in the west of the region would substantially restrict their distribution.

Large carnivorous species range over disproportionately large areas. For example, the home ranges of *Varanus gouldii* on Kangaroo Island averaged 25 ha compared with 14 ha predicted by Turner *et al* (1969) equation (Green and King 1978). A *Varanus varius* monitored by radio telemetry had a calculated home range (based on three 'capture' points per day) of 300 ha (data from Stebbins and Barwick 1968) compared with a predicted 74 ha. Hence the area of The Rock approximates the home range of one large lace monitor.

In the wheat belt of Western Australia, Kitchener *et al.* (1980) recorded sand goannas, with one exception, only on reserves larger than 1500 ha and they recommended that this area be taken as the minimum reserves size for conservation of lizards. In the wheat-belt of the south-western slopes, all but three forests are smaller than 1500 ha. Buckingbong is the only forest of any size, equalling in area the sum of all the other forests in the west of the region. Many of the other forests are less than 400 ha, and all are disjunct and surrounded by agriculture.

The forests of the central zone are also isolated but the intervening country is principally pastoral land. The area surveyed (65 km²) represents about a quarter of the remaining forest in this zone.

In the east, the forests are much more extensive. The area surveyed was 385 km² and there is at least three times as much forest again. In addition many of the forests are joined by corridors of similar country.

We conclude, therefore, that the south-western slopes contains marginal representation of two faunas across a zone of transition, and that the forests in the region serve more to maintain the range of species than to provide core conservation areas. In the east of the region, the extent of forests allows us to be confident of the conservation of fauna there. However, in the west the fauna is depauperate, dispersal is restricted by agriculture, and the majority of the forests are small, casting doubt on their value for conservation. In the wheat country, only Buckingbong may be large enough to preserve its total herptofauna.

ACKNOWLEDGEMENTS

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APPENDIX 1. List of frogs collected in forests on the southwestern slopes coded as in Table 1.

Species	A	B	C	D	E	F	G	H	I	J	K	L
Leptodactylidae												
<i>Limnodynastes convexiusculus</i> *			?									
<i>Limnodynastes dumerillii</i>	x	x	x									
<i>Limnodynastes fletcheri</i>												x
<i>Limnodynastes interioris</i>				x			x	x	x			
<i>Limnodynastes peronii</i>	x	x										
<i>Limnodynastes tasmaniensis</i>	x	x	x	x		x	x	x	x			x
<i>Pseudophryne bibronii</i>	x	x	x	x	x							
<i>Ranidella</i> spp.	x	x	x	x	x	x	x	x	x		x	x
<i>Uperoleia marmorata</i>	x											
<i>Uperoleia rugosa</i>									x	x		
Hylidae												
<i>Litoria booroolongensis</i>	x	x										
<i>Litoria ewingii</i>		x										
<i>Litoria peronii</i>	x	x	x	x		x		x	x		x	x
<i>Litoria raniformis</i>		x							x		x	x
<i>Litoria verreauxii</i>	x		x									
TOTAL	9	9	6	5	2	3	3	4	6	1	3	5

**Limnodynastes convexiusculus* — a specimen collected in Tumut State forest has tentatively been identified as this species by the Australian Museum (R87657), despite its range being tropical coastal Australia. We suspect it to be a variant of *Limnodynastes tasmaniensis* and have not included it in subsequent analyses.

ZOOGEOGRAPHICAL TRANSITION AND CONSERVATION

APPENDIX 2. List of reptiles collected in forests on the southwestern slopes coded as in Table 1.

Species	A	B	C	D	E	F	G	H	I	J	K	L
Chelonidae												
<i>Chelodina expansa</i>												x
<i>Chelodina longicollis</i>											x	
<i>Emydura macquarii</i>												x
Gekkonidae												
<i>Diplodactylus intermedius</i>							x		x	x		
<i>Diplodactylus vittatus</i>		x			x			x				
<i>Phyllodactylus marmoratus</i>				x	x		x			x	x	
Pygopodidae												
<i>Lialis burtonis</i>							x					
Agamidae												
<i>Amphibolurus barbatus</i>					x			x	x			
<i>Amphibolurus muricatus</i>		x	x	x	x	x						
Varanidae												
<i>Varanus gouldii</i>							x		x			
<i>Varanus varius</i>		x	x	x	x	x	x	x	x			
Scincidae												
<i>Carlia tetradactyla</i>			x	x	x	x						
<i>Cryptoblepharus boutonii</i> *						x		x				
<i>Cryptoblepharus carnabyi</i>							x		x	x		
<i>Ctenotus robustus</i>					x							
<i>Ctenotus strauchii</i>								x	x			
<i>Ctenotus taeniolatus</i>		x		x	x	x						
<i>Egernia cunninghami</i>		x		x								
<i>Egernia striolata</i>	x	x		x	x			x				
<i>Egernia whitii</i>	x											
<i>Hemiergis decresiensis</i>	x	x	x									
<i>Lampropholis delicata</i>	x											
<i>Lampropholis guichenoti</i>	x	x	x	x	x							
<i>Leiopisma platynota</i>		x	x									
<i>Leiopisma trilineata</i>	x											
<i>Lerista bougainvillii</i>		x										
<i>Lerista muelleri</i>								x	x			
<i>Morethia boulengeri</i>			x	x	x		x	x	x	x		
<i>Sphenomorphus tympanum</i>	x	x	x	x								
<i>Tiliqua nigrolutea</i>	x											
<i>Tiliqua scincoides</i>	x	x							x			
<i>Trachydosaurus rugosus</i>				x								
Typhlopidae												
<i>Typhlina nigrescens</i>		x										
Elapidae												
<i>Cryptophis nigrescens</i>		x										
<i>Demansia psammophis</i>					x							
<i>Drysdalia coronoides</i>	x											
<i>Pseudechis porphyriacus</i>	x	x	x	x	x	x					x	x
<i>Pseudonaja textilis</i>		x			x			x	x	x		
TOTAL	11	16	9	12	14	6	7	9	10	5	3	3

*Specimens were not taken from these areas and identification to current taxa within the previous species *Cryptoblepharus boutonii* is not possible.

A Survey of the Mammals of Mount Royal and Barrington Tops, New South Wales

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ABSTRACT

This paper reports the results of a survey of the terrestrial mammals of Mount Royal and Barrington Tops in east-central New South Wales. A total of 30 species (23 native, 7 introduced) was recorded from the two areas. Twenty-four species were recorded from Mount Royal, including one individual of the rare Hastings River Rat *Pseudomys oralis*, while 15 species were recorded from Barrington Tops. Two methods were used to increase the probability of capture of *P. oralis*. First, ecologically similar species of rats were removed from trapping lines, hence reducing possible competition for traps and interspecific competition. Second, hair analysis was carried out to unequivocally distinguish *P. oralis* from the more abundant but morphologically similar Bush Rat *Rattus fuscipes*. Both methods could be of general use in field survey.

INTRODUCTION

Between 20 and 28 October 1984, a survey of mammals was carried out at Mount Royal and Barrington Tops in east-central New South Wales. The major aim of the survey was to locate populations of the Hastings River Rat, *Pseudomys oralis*, but other species were also recorded during routine trapping and spotlighting. Neither area has been surveyed previously for mammals; the nearest published records appear to be from the Allyn River 10 km to the south of Barrington Tops (Marlow 1958), from the Manning River 20 km to the north of the Tops (Hyem 1979), and from the Comboyne Plateau over 100 km to the north-east (Chisholm 1925).

STUDY AREAS

MOUNT ROYAL

This study area was centred at Mount Royal (alt. 1184m, 32°10'S, 151°20'E) on the south-western slopes of the Barrington Plateau, 51 km north of Singleton

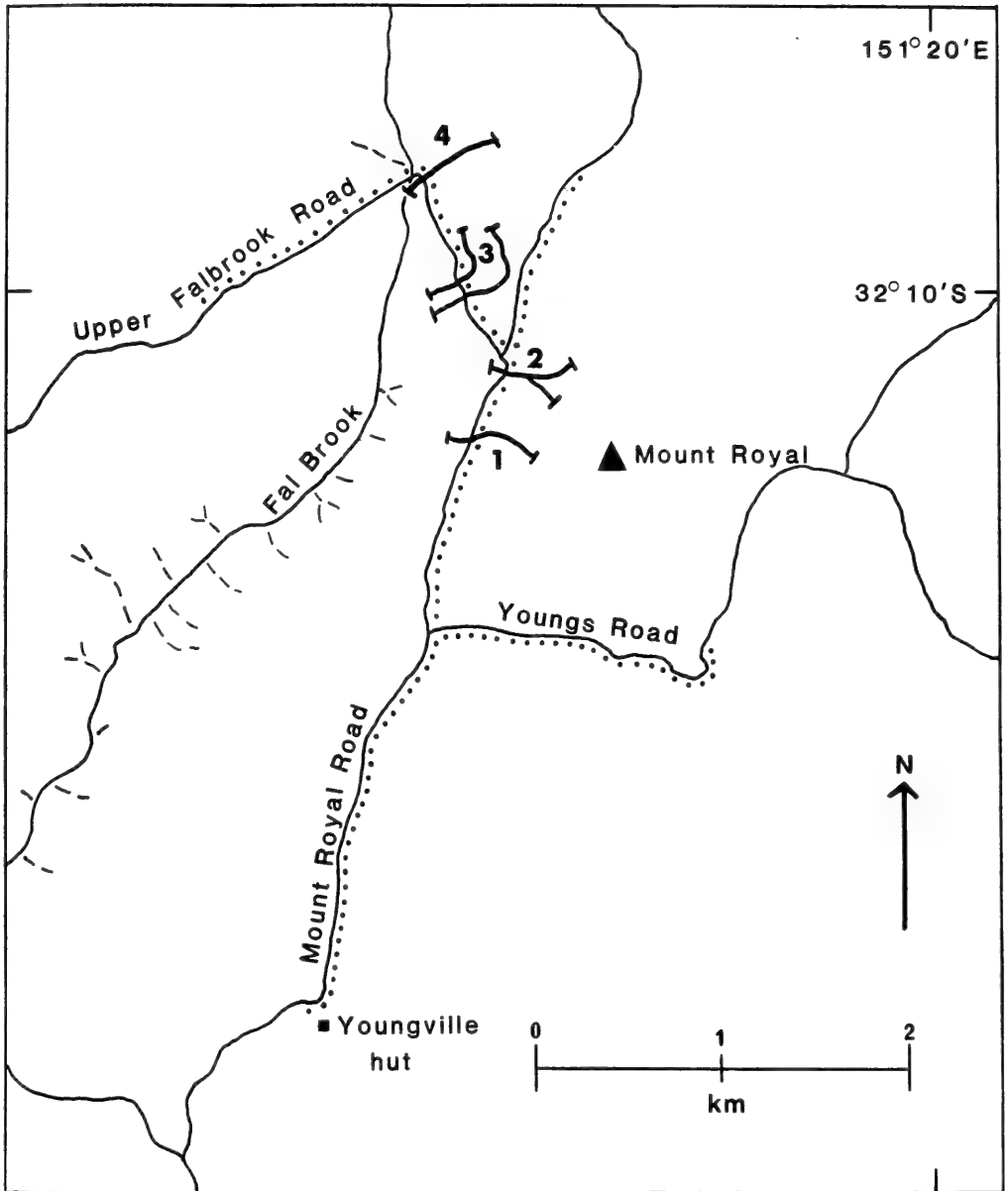


Fig. 1. The Mount Royal study area, with place names mentioned in the text. The small mammal trap lines are numbered, and the spotlighting transect is shown by a dotted line.

MAMMALS OF MOUNT ROYAL AND BARRINGTON TOPS

(Fig. 1). The Mount Royal area provides a mosaic of habitats from closed forest to dry open-forest, and tall open-forest to swamp, with a corresponding spectrum of ecotones.

Closed forest (sensu Specht 1970) occurs patchily throughout this study area, but is densest along the middle and lower reaches of creeks. The dominant closed forest species are *Dysoxylum fraserianum*, *Doryphora sassafras*, *Ackama paniculata*, *Heritiera actinophylla* and *Toona australis*, with a sparse understory of vines and shrubs: *Smilax glyciophylla*, *Cephalalaria cephalobotrys* and *Ripogonum discolor*. Bracken *Pteridium esculentum*, other ferns and fallen logs, form ground cover on the forest edges.

Tall open-forest often borders closed forest, and is characterized by *Eucalyptus* spp., including *E. laevopinea*, with a dense understory of bracken, *Leptospermum* spp. and *Blechnum nudum*.

Open-forest also occurs patchily at Mount Royal and characterizes the steeper slopes and upper reaches of creeks. The open-forest is dominated by *Eucalyptus andrewsii*, *E. macrorrhyncha* and *E. cameronii*, with an understory of *Acacia* spp., *Xanthorrhoea australis*, bracken and tussock grass.

Swamps occur where creeks flow through gently sloping areas of open-forest. *Leptospermum* sp. is often the dominant shrub in the swamps, but dense ground cover is provided by bracken, *B. nudum*, *Carex gaudichaudiana*, *Cyperus* sp. and unidentified grasses.

Except for the rainforest gullies, all forest areas have been burnt within the last 2-4 years, and are currently subject to light, intermittent grazing by cattle.

BARRINGTON TOPS

This study area was located on the southern edge of the Barrington Plateau near Carey's Peak (alt. 1544m, 32°03'S, 151°27'E), 17 km north-east of Mount Royal (Fig. 2). The principal habitats are closed forest, open-forest and swamp.

Closed forest occurs mostly on the middle and lower slopes of creeks, and is always dominated by *Nothofagus moorei*. Except for clumps or isolated specimens of *Polygonum* sp. and *Dicksonia antarctica*, the understory is sparse and comprises similar species to those at Mount Royal.

Open-forest is widely distributed from the low-lying swamps to the ridges, and is always dominated by snowgum *Eucalyptus pauciflora*, with a moderate to dense understory of *Tasmannia purpurea*, *Leptospermum minutifolium* and *Acacia* spp.

Swamps (Fig. 2) are dominated by *Orites* and *Hakea* spp., *Lomandra longifolia* and *Restio stenocoleus* on the drier fringes, with *Cyperus* sp., sedges and *Sphagnum* in poorly drained areas.

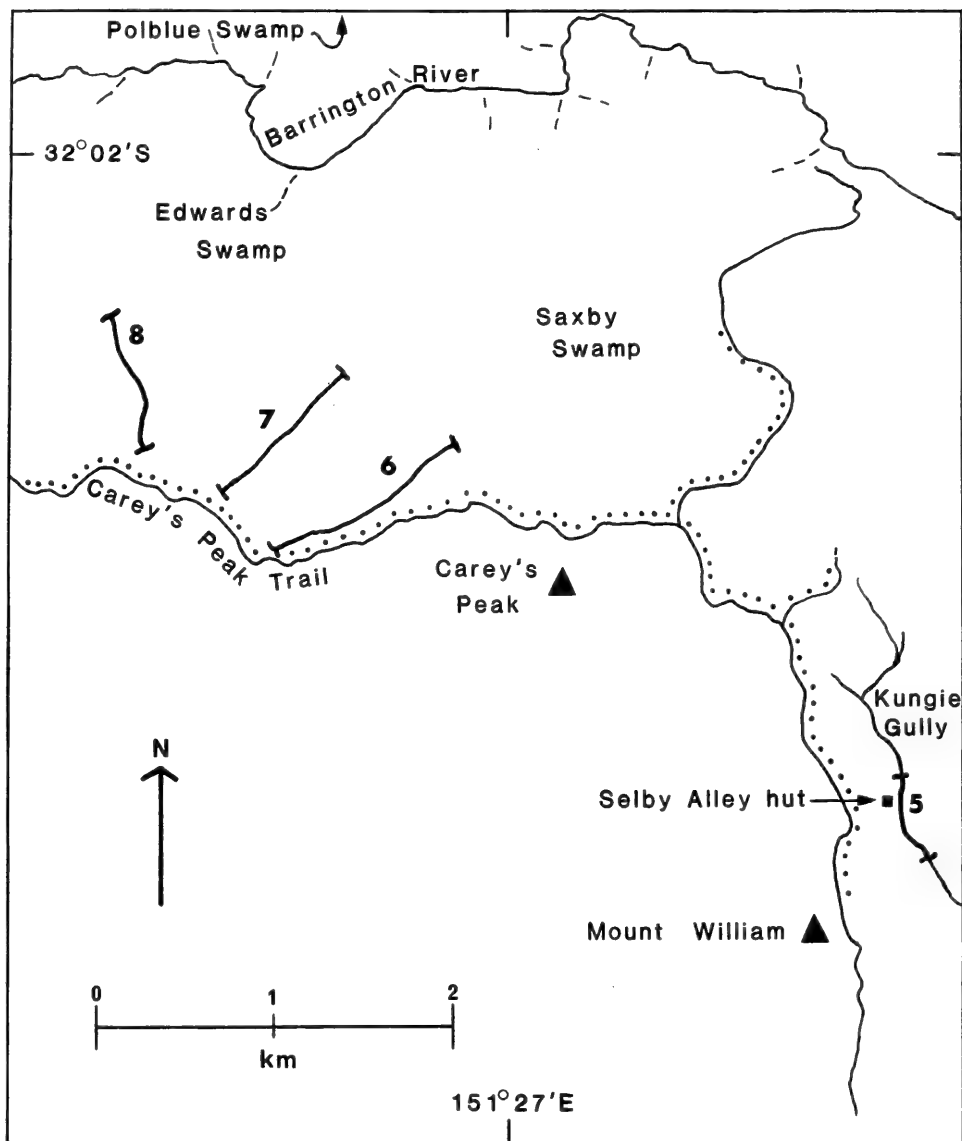


Fig. 2. The Barrington Tops study area. Symbols are as in Fig. 1.

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There is no recent fire history in this part of Barrington Tops, and cattle are excluded.

METHODS

Four trap lines for small mammals were established along creeks in each study area, to sample each of the habitat types described above (Figs. 1 and 2). Elliott folding aluminium traps (33x10x10cm) were set singly at intervals of about 10 m along the lines, baited with a mixture of oats, peanut butter, honey and sultanas, and provided with dry grass or leaves for bedding. Captured animals were identified to species, sexed, weighed and inspected for reproductive condition. To identify recaptured animals, a clipping of fur was taken from the left or right flank or middle of the back. Traps were cleared in the morning soon after dawn and reset with fresh bait and bedding.

While *Antechinus* and other non-*Rattus* species were released at the point of capture, the Bush Rat *R. fuscipes* and the Swamp Rat *R. lutreolus* were removed from the trap lines at Mount Royal and released in suitable habitat elsewhere. It was hoped that this would reduce competition for traps and also possible competition between species (see King 1984, Fox and Pople 1984), and hence enhance the probability of capture of *P. oralis*. Due to wet weather and logistical difficulties, species displacement was not attempted at Barrington Tops.

Adult *R. fuscipes* is longer and heavier than *P. oralis*, but otherwise the two species are very similar in appearance (Watts and Aslin 1981). Consequently, to unequivocally identify *P. oralis* from *R. fuscipes*, head-body and tail measurements were taken from captured rats by holding them against a measuring rule. As a further measure, clippings of fur were retained from all captured rats, and later identified using the methods and keys in Brunner and Coman (1974).

Large terrestrial mammals and arboreal species were recorded by spotlighting, droppings or other miscellaneous methods (e.g. daytime sightings, field signs).

Spotlighting was carried out along tracks in each study area (Figs 1 and 2) from a slowly moving vehicle using a hand held sealed beam spotlight.

RESULTS

A total of 30 species (23 native, 7 introduced) was recorded from Mount Royal and Barrington Tops. These are listed, following the nomenclature of Strahan (1983), in Table 1. For clarity, we present more detailed notes on each species separately for the two study areas.

MOUNT ROYAL

Twenty-four species were recorded between 20 and 23 October, 1984 (Table 1). Over the four day sampling period, trapping effort for small mammals

TABLE 1. Systematic list of the mammals recorded at Mount Royal and Barrington Tops. Recording methods: T = trapping; S = spotlighting; M = miscellaneous; D = droppings; R = reported sighting.

Common name	Scientific name	Mount Royal	Barrington Tops
	Order Monotremata		
1. Short-beaked Echidna	<i>Tachyglossus aculeatus</i> (Shaw)	M	
2. Platypus	<i>Ornithorhynchus anatinus</i> (Shaw)		R
	Order Marsupialia		
3. Brown Antechinus	<i>Antechinus stuartii</i> Macleay	T	T
4. Dusky Antechinus	<i>Antechinus swainsonii</i> (Waterhouse)		T
5. Brush-tailed Phascogale	<i>Phascogale tapoatafa</i> (Meyer)		T
6. Spotted-tailed Quoll	<i>Dasyurus maculatus</i> (Kerr)	R	
7. Sugar Glider	<i>Petaurus breviceps</i> Waterhouse	S	
8. Yellow-bellied Glider	<i>Petaurus australis</i> Shaw	S	
9. Greater Glider	<i>Petauroides volans</i> (Kerr)	S	
10. Common Ringtail Possum	<i>Pseudocheirus peregrinus</i> (Boddaert)	S	S
11. Common Brushtail Possum	<i>Trichosurus vulpecula</i> (Kerr)	S	
12. Red-necked Pademelon	<i>Thylogale thetis</i> (Lesson)	S	
13. Swamp Wallaby	<i>Wallabia bicolor</i> (Desmarest)	M	
14. Rufous Bettong	<i>Aepyprymnus rufescens</i> (Gray)	S	
15. Eastern Grey Kangaroo	<i>Macropus giganteus</i> Shaw	M	M
16. Red-necked Wallaby	<i>Macropus rufogriseus</i> (Desmarest)	S, M	
17. Common Wombat	<i>Vombatus ursinus</i> (Shaw)		R
	Order Rodentia		
18. Bush Rat	<i>Rattus fuscipes</i> (Waterhouse)	T	T
19. Swamp Rat	<i>Rattus lutreolus</i> (Gray)	T	
20. Hastings River Rat	<i>Pseudomys oralis</i> Thomas	T	
21. Fawn-footed Melomys	<i>Melomys cervinipes</i> (Gould)	T	T
22. Broad-toothed Rat	<i>Mastacomys fuscus</i> Thomas		T
23. Water-rat	<i>Hydromys chrysogaster</i> Geoffroy	M	M
	Order Lagomorpha		
24. Rabbit	<i>Oryctolagus cuniculus</i> (L.)	S, M	
	Order Carnivora		
25. Feral Cat	<i>Felis catus</i> L.	S	
26. Fox	<i>Vulpes vulpes</i> (L.)	D	D
27. Dog or Dingo	<i>Canis familiaris</i> L.	D	D
	Order Artiodactyla		
28. Feral Pig	<i>Sus scrofa</i>	M	M
29. Cattle	<i>Bos taurus</i>	M	
	Order Perissodactyla		
30. Horse	<i>Equus caballus</i>		M

totalled 1065 trap nights and resulted in 124 captures of five species. Spotlighting totalled 7h.

1. Echidna, *Tachyglossus aculeatus*. One individual was seen near line 4.

3. Brown Antechinus, *Antechinus stuartii*. Thirty-two *A. stuartii* were captured a total of 52 times, giving an overall trap success of 4.8%. All individuals were

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females with pouch young, with a mean body weight of $28.5 \pm 2.3\text{g}$ ($n=30$). Each female had 8 nipples and 0-8 young. The crown-rump lengths of the young were 9.5–13.0mm, indicating that mating had occurred in late August or early September. Although this species was captured in all habitats on each line, most captures occurred near swamp areas on line 3.

6. Spotted-tailed Quoll, *Dasyurus maculatus*. One specimen has been taken in the last year near Mount Royal (D. Hardman, *personal communication*).

7. Sugar Glider, *Petaurus breviceps*. Three individuals were observed in a mature smoothbark eucalypt in open-forest on Mount Royal Road.

8. Yellow-bellied Glider, *Petaurus australis*. Single individuals were observed in mature eucalypts bordering closed forest on two separate occasions along Upper Falbrook Road.

9. Greater Glider, *Petauroides volans*. Two individuals were observed on one night in mature eucalypts about $\frac{1}{2}$ km apart along Upper Falbrook Road.

10. Ringtail Possum, *Pseudocheirus peregrinus*. One individual was observed nesting in an open forest/closed forest ecotone at the end of the spotlighting transect on Upper Falbrook Road.

11. Brushtail Possum, *Trichosurus vulpecula*. Single individuals were observed on two separate occasions in open and tall open-forest near the Youngville hut and along Mount Royal Road.

12. Red-necked Pademelon, *Thylogale thetis*. Several were seen near the Youngville hut and on the Upper Falbrook Road, where grassy patches are adjoined by forest.

13. Swamp Wallaby, *Wallabia bicolor*. One individual was disturbed during small mammal trapping along line 1.

14. Rufous Bettong *Aepyprymnus rufescens*. One individual was observed on a small clearing in closed forest where Fal Brook crosses Upper Falbrook Road.

15. Eastern Grey Kangaroo, *Macropus giganteus*. Several were observed throughout the length of the spotlighting transect in patches of grass or bracken within open-forest.

16. Red-necked Wallaby, *Macropus rufogriseus*. This species occurred abundantly in open-forest throughout the length of the spotlighting transect.

18. Bush Rat, *Rattus fuscipes*. This species accounted for almost half the total captures of small mammals (60), and occurred in all habitats on each of the trap lines. No displaced rats returned during the four day trapping period, but overall trap success remained similar each day: day 1, 5.8%; day 2, 5.7%; day 3, 5.7%; day 4, 5.4%. This may indicate that new *R. fuscipes* moved onto

the trap lines, or that resident individuals progressively overcame trap shyness over the trapping period. All males had scrotal testes and all females were mated (vagina open, bruised or bloody), pregnant or lactating. Mean body weight and length were greater in males than in females (Table 2).

19. Swamp Rat, *Rattus lutreolus*. Ten individuals were captured, all on or near sedge swamps on lines 1 and 3. Swamp Rats were first captured on the third day of trapping, with no individuals displaced on day 3 subsequently returning. All males were scrotal and all females mated or pregnant. The mean body weights and head-body lengths of male and female *R. lutreolus* were comparable with those of *R. fuscipes*, but tail lengths were shorter (Table 2).

TABLE 2. Body sizes of captured rats. Means are given \pm standard deviation (N).

Weight (g)		Head-body length (mm)	Tail length (mm)
<i>Rattus fuscipes</i>		Mount Royal	
♂	143.2 \pm 11.4 (37)	159.4 \pm 9.5 (35)	154.5 \pm 8.0 (35)
♀	125.3 \pm 13.6 (22)	143.9 \pm 6.7 (22)	146.4 \pm 10.7 (21)
<i>R. fuscipes</i>		Barrington Tops	
♂	155.1 \pm 8.3 (41)	164.8 \pm 11.2 (38)	160.6 \pm 12.1 (38)
♀	129.7 \pm 14.2 (33)	152.0 \pm 10.8 (30)	148.3 \pm 9.1 (30)
<i>R. lutreolus</i>		Mount Royal	
♂	145.5 \pm 9.6 (6)	159.7 \pm 5.5 (3)	108.3 \pm 7.6 (3)
♀	124.0 \pm 7.0 (4)	145.0 \pm 5.0 (3)	98.3 \pm 2.9 (3)
<i>Mastacomys fuscus</i>		Barrington Tops	
♂	142.3 \pm 12.0 (6)	155.3 \pm 5.4 (4)	119.8 \pm 9.6 (4)
♀	126.7 \pm 10.3 (6)	147.5 \pm 6.2 (4)	117.3 \pm 7.4 (4)

20. Hastings River Rat, *Pseudomys oralis*. One individual was captured on the second day of trapping on line 3. Apart from having a bi-coloured tail, this animal strongly resembled *R. fuscipes* and lacked both the snub nose and dark eye ring which are supposedly typical of *P. oralis* (Covacevich and Easton 1974, Kirkpatrick 1983). The animal, a female, was similar in length to female *R. fuscipes* (head-body length 140 mm, tail length 140 mm; compare Table 2), but less massive (90g) and not in reproductive condition. Subsequent analysis of the hair of this animal confirmed that it differed in gross appearance, cuticular structure and cross section from the hairs of all *R. fuscipes* and *R. lutreolus* captured, but that it was identical to hairs from a male *P. oralis* in the Australian Museum (an uncatalogued specimen from the Blick's River Forest Reserve).

The trap capturing *P. oralis* was located under a large rotting log amid *Blechnum nudum* at the lower, swampy end of line 3. This local area shares some floristic similarity to the Blick's River and Forbes River sites where other *P. oralis* have been captured (Hughes 1982, King 1984), but differs in that it was poorly drained with only a trickle of running water.

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21. Fawn-footed Melomys, *Melomys cervinipes*. One pregnant female, weighing 102g, was captured in a closed forest gully on line 2 on the third day of trapping.

23. Water-rat, *Hydromys chrysogaster*. A small cairn of crustacean remains, probably characterizing a feeding site of the Water-rat, was found on the bank of Fal Brook 50 m downstream of where the brook crosses the road.

24. Rabbit, *Oryctolagus cuniculus*. Rabbits were observed throughout the study area on grassy verges and the edge of open-forest.

25. Feral Cat, *Felis catus*. One cat was observed on Upper Falbrook Road near trap line 4.

26. Fox, *Vulpes vulpes*. Five droppings were collected from Youngs Road and Upper Falbrook Road. These contained hairs and bone fragments of *Rattus* spp and possibly *Antechinus*.

27. Dog or Dingo, *Canis familiaris*. Dog droppings were found near the Youngville hut. These contained no hairs and were possibly from domestic pets.

28. Feral Pig, *Sus scrofa*. Disturbance by pigs was evident on trap lines 1, 2 and 4.

29. Cattle, *Bos taurus*. Cattle are allowed to graze throughout the Mount Royal State Forest. Two groups comprising 4-6 individuals were observed near the Youngville hut.

In addition to these confirmed records, the presence of bandicoots (*Isoodon macrourus* (Gould) or *Perameles nasuta* (Geoffroy) was suspected due to many conical holes that had been dug in the ground in grassy open-forest areas.

BARRINGTON TOPS

A total of 15 species was recorded between 25 and 28 October, 1984 (Table 1). Trapping effort for small mammals totalled 950 trap nights and resulted in 206 captures of six species of small mammals. Spotlighting totalled 2h.

2. Platypus, *Ornithorhynchus anatinus*. Platypus have been recorded in the Barrington River at Rawdon Vale in the last year (D. Upton, *personal communication*).

3. Brown Antechinus, *Antechinus stuartii*. Seven individuals were captured 15 times on lines 5, 6 and 8 in either the closed forest edge or snowgum woodland, with an overall trap success of 1.6%. All animals were females with eight nipples and 6-8 pouch young, with a mean body weight of 29.6 ± 2.1 g ($n=7$). The crown-rump lengths of the young were only 8.0–10.0 mm, indicating that mating had occurred later than at Mount Royal, between early and mid-September.

4. Dusky Antechinus, *Antechinus swainsonii*. A lactating female with eight nipples (41g) was captured on the third day of trapping in an ecotone area on line 8 between open swamp and woodland with a heath understory.

5. Brush-tailed Phascogale, *Phascogale tapoatafa*. Two females were captured on the second and third days of trapping, at altitudes of 1480 and 1500 m in closed forest on line 6. The first animal (171g) was probably at the end of lactation and had a pink, sparsely haired pouch with six prominent nipples. The second animal (150g) had a well-developed pouch, but escaped before more detailed observations were made.

10. Common Ringtail Possum, *Pseudocheirus peregrinus*. One individual was observed in snowgum woodland near Carey's Peak.

15. Eastern Grey Kangaroo, *Macropus giganteus*. Several were observed in open snowgum woodland between Carey's Peak and the end of the spotlighting track

17. Common Wombat *Vombatus ursinus*. Wombats have been observed on Carey's Peak Trail near Mount William (D. Upton, *personal communication*).

18. Bush Rat, *Rattus fuscipes*. Seventy-four *R. fuscipes* were captured a total of 164 times, making this species the most abundant in the study area. Rats occurred in all habitats except open swamp on each of the four trap lines. Recapture success rose from 15.8% on day 2 (38 captures, 6 recaptures) to 85.9% on day 4 (64 captures, 55 recaptures), suggesting that the majority of the trappable population had been captured.

Mean body weights and lineal measurements were comparable with those for the Mount Royal population (Table 2), and all males and females were in similar reproductive condition. However, unlike the Mount Royal population, some rats at Barrington Tops had a white tip on the terminal 5–10 mm of the tail. This was present in 13.5% of all captured rats, and perhaps represents a polymorphism or fungal skin disease.

21. Fawn-footed Melomys, *Melomys cervinipes*. One scrotal male, weighing 115g, was captured in dense, steep-sided rainforest along line 5 on the fourth day of trapping.

22. Broad-toothed Rat, *Mastacomys fuscus*. Thirteen *M. fuscus* were trapped on Saxby and Edwards Swamps, at the bottom ends of lines 6, 7 and 8. Both sexes were in reproductive condition, and comparable in size to *R. lutreolus* (Table 2), which this species apparently replaces at high altitude. Recapture success rose from 20% on day 3 (10 captures, 2 recaptures) to 72.7% on day 4 (11 captures, 8 recaptures), suggesting that most of the trappable population had been captured.

MAMMALS OF MOUNT ROYAL AND BARRINGTON TOPS

23. Water-rat, *Hydromys chrysogaster*. A feeding site, comprising piles of crustacean remains, was found on the bank of a steep fast-flowing section of Kungie Gully, 70m downstream of the Selby Alley hut.

26. Fox, *Vulpes vulpes*. Twenty droppings were collected from along vehicle tracks and walking trails across the swamps. Two comprised the remains of crustaceans, the remaining 18 contained the hair and bones of *R. fuscipes*, *M. fuscus*, and an unidentified bat.

27. Dog or Dingo, *Canis familiaris*. Two droppings were found near Carey's Peak. These contained *Rattus* hairs only.

28. Feral Pig, *Sus scrofa*. Pig disturbance was obvious in all wooded habitats but not on the swamps.

30. Horse, *Equus caballus*. A small group of horses was seen in the northern part of the study area at Polblue Swamp.

DISCUSSION

This short but intensive survey revealed a very high diversity of terrestrial mammal species at Mount Royal and Barrington Tops. Although no attempt was made to define the geographical extent of either study area, the 30 species recorded compare favourably with a total of 14 species (excluding macropods) recorded by Hyem (1979) from the Manning River, and 25 species (including one bat) recorded by Chisholm (1925) from the Comboyne Plateau. Maynes (1977) further reported the presence of the Parma Wallaby, *Macropus parma*, from Barrington Tops, although this species was not observed in the present study, with further survey effort, there is little doubt that more species of macropods, small possums, gliders and bandicoots would also be found. The trapping methods were not appropriate for capturing other, trap-shy, species which were potentially present (e.g. the Common Dunnart, *Sminthopsis murina*; see Archer 1979, 1981); moreover, no attempt was made to census bats.

The capture of *P. oralis* at Mount Royal is the southern-most locality record for this rare species, and only the third locality record for New South Wales. Apparently suitable habitat for *P. oralis* occurs patchily throughout the Mount Royal area. This, and the finding of (recent?) *P. oralis* remains in an owl pellet on farmland 9 km south of Mount Royal (I. Cranwell, *personal communication*), suggest that sparse populations of this species may occur elsewhere in the Mount Royal range. The captures of *M. cervinipes* and *R. lutreolus* at Mount Royal are probably near the western-most limits for these species (Watts and Aslin 1981).

The range of habitats at Barrington Tops is comparable with that at Mount Royal and, while *P. oralis* was not trapped there, apparently suitable habitat is found in the heath communities around watercourses which drain into the main

swamps. The survey at Barrington confirmed the status of the *M. fuscus* population (the northernmost in Australia), and produced an apparent altitudinal record (1500m) for *P. tapoatafa* (Cuttle 1983). These records, and the high overall diversity of mammal species, indicate that the Mount Royal — Barrington Tops area is of great conservation value, and should be managed accordingly.

Two further points emerged from this survey. First, in trapping for *P. oralis*, the probability of capture may be enhanced if ecologically similar sympatric species (e.g. *R. fuscipes*) are removed from trap lines. Second, there is clear merit in using hair analysis to positively distinguish *P. oralis* from the ubiquitous *R. fuscipes*. Indeed, Bush Rats may so resemble *P. oralis* (even, in some populations, in having bi-coloured tails: A. B. Rose, *personal communication*) that the latter species could otherwise be easily overlooked in field survey.

ACKNOWLEDGEMENTS

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Notes on Capture Techniques for Small Mammals of the Arid Zone

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The arid zone dasyurids *Planigale gilesi* and *P. tenuirostris* are currently regarded as sparse because they are seldom captured in large numbers. This sparseness may be a true reflection of their rarity or due to their poor response to the capture techniques employed. In reported studies, Sherman and Elliott traps have been successful for *P. gilesi* individuals (Aitken 1972, Denny 1975) but captures of *P. tenuirostris* were only effected with the pitfall technique and their numbers were always less than *P. gilesi* (Denny *et al.* 1979).

Presented here are the results of tests on new variations and modifications of the two techniques.

THE STUDY AREAS

Two of the three tests (A and B) were at Fowlers Gap Station, 110 km north of Broken Hill, and the third (C) was at Mt. King in the Sturt National Park, Tibooburra, N.S.W.

Test A was in a habitat of tussock grassland, principally *Astrebla pectinata*, on deep red massive sandy loam soils and the habitat for Test B was a shrubland of copperburrs (*Sclerolaena* Spp.) with other chenopods (Mabbutt *et al.* 1973). At Mt. King the tussock grassland habitat was very similar to that for Test A and Mitchell grass (*Astrebla* spp.) dominated (Anon 1979).

MATERIALS

The aluminium Elliott traps used were the Type A (Elliott Scientific Equipment, Upwey, Victoria) which measure 33 x 9 x 10 cm. All trigger plates were adjusted to trip with a static loading of 2 gm and were set 5 mm from the trap floor.

The pitfall technique had two components: the pit-traps and the drift fence connecting the pits. Pit-traps were of two types. The majority were constructed from 26 g galvanized plate curved to form a cylinder approximately 20-25 cm

in diameter and 35-40 cm deep. A second type were plastic; either household 2 gallon buckets or equivalent sized plant pots. Placement of metal and plastic pits was random in all tests. Drift fences were constructed from fiberglass insect screening and stood 30 cm high. Previous experience with strips of black polythene sheeting found this material to be unsatisfactory.

METHODS

TEST A

This test investigated two types of drift fence and two modifications to the pitfall traps: covered and uncovered. Three lines of pitfall traps were deployed in random alignment with approximately 500 m between lines. These lines were trapped concurrently for 15 consecutive days during February, 1979.

The first drift line (No. 1) had a profile shown in Fig. 1, a and spanned 19 pits spaced 10 m apart. All odd numbered pits were covered with a wooden lid approximately 1 cm thick and larger than the pit diameter by at least 5 cm.

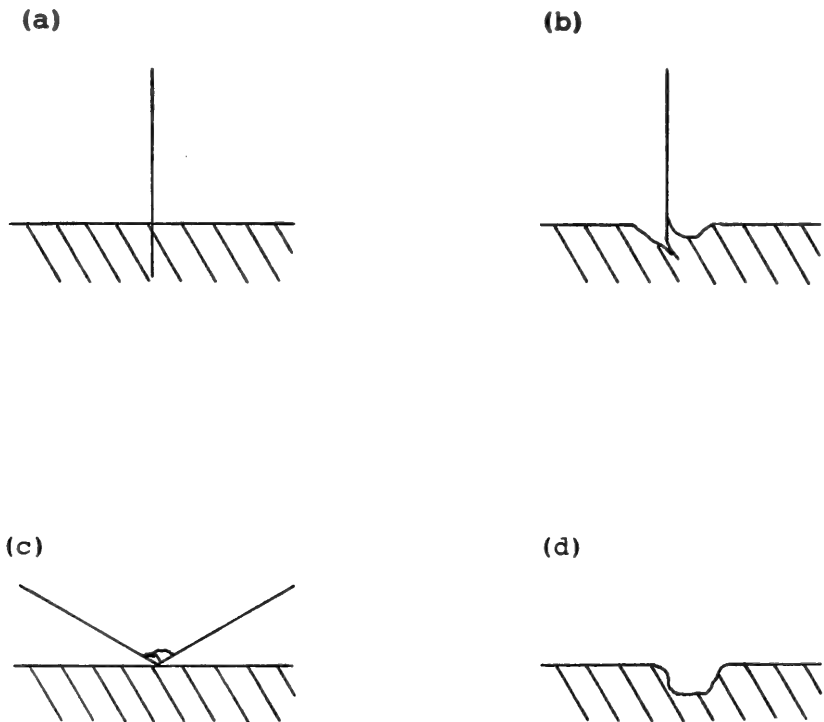


Fig. 1. Profiles of drift lines used in the tests. Soil is shown by shading and descriptions are given in the text.

ARID ZONE MAMMAL CAPTURE TECHNIQUES

Small stones kept these lids clear of the pit top by about 4 cm so that small mammals had access to the pit from all directions. Even numbered pits were left exposed.

Pits on the second line (No. 2) were not covered. The fence profile was the same as the first one (Fig. 1, a) and it spanned 20 pits spaced 10 m apart.

At the third line (No. 3) there was no fence but only a shallow trench connecting the 9 pits (Fig. 1, d). These pits were 10 m apart and the trench was approximately 5-8 cm wide and deep.

TEST B

This test compared modified Elliott traps and pitfall traps with a drift fence. Modifications were of three types and 25 traps of each were set 10 m apart in three lines radiating from a common point. The line of 15 pitfall traps spaced at 10 m intervals commenced at this point and the drift fence had a profile shown in Fig. 1, b. Each modified trap was aligned randomly and matched with a standard Elliott set 30 cm away with the entrances facing each other. Bait in all Elliotts was a mixture of peanut butter, rolled oats, fried bacon pieces and raisins. All lines except type (iii) below, were trapped concurrently for 13 consecutive days during May 1979. Those of type (iii) were trapped concurrently for only 10 days. Modifications to the Elliotts were as follows:

(i) The solid metal rear door was replaced with a metal door containing a wire mesh covered hole 50 mm in diameter. This mesh was of 0.5 mm wire formed into 5 mm squares.

(ii) Traps were modified as in (i) and with denim material glued onto the outside of the entrance door, floor space from the latched door to the trigger plate and on the trigger plate.

(iii) Traps with the standard solid rear door and with denim attached as in (ii).

The denim was intended to provide a more natural feel to the animals' feet than that of the metal surface.

TEST C

Three lines of different drift fences were compared with simultaneous trapping with unmodified Elliott traps of 16 consecutive days in July 1979. Profiles of the fences are shown in Fig. 1; b, c and d.

The parallel drift lines were set 50 m apart and each spanned 43 pits in their length of 200 m. Centrally placed between these lines was a grid of 243 Elliott traps set in 17 rows of 14 traps. A final row contained only 5 traps. The distance between traps and between rows was 10 m. Bait in the Elliott traps was the same mixture as used in Test B.

RESULTS AND DISCUSSION

Trap success and the numbers of captures of Test A, B, C are given in Tables 1, 2, 3 respectively. Unfortunately captures were too few to allow statistical comparisons. However, the tests B and C indicate that the pitfall technique was superior overall to the Elliott traps in the capture of the small dasyurids. Elliott traps were the more successful technique in the capture of the introduced rodent, *Mus musculus*. Such a bias in the techniques towards either of the two families of small mammals show that there is no generalized unbiased survey method.

The trap success given in Table 1 indicates that a covered pitfall trap offers no improvement in trap efficiency. In a similar comparison to Test A, Braithwaite (1983) found both types of trap caught the same components of the vertebrate fauna but traps without a cover were more effective.

Night observations on the response of released individuals suggest that the type of drift fence profile is important to the success of pitfall traps. Individuals of *P. gilesi*, *P. tenuirostris* and *Sminthopsis crassicaudata* followed the fence type shown in Fig. 1, c for distances of 4-5 m which was about twice the distance

TABLE 1. Captures of each species during Test A.

Species	No. 1 Drift Line Covered Pits	No. 2 Drift Line Uncovered Pits	No. 3 Drift Line
<i>S. crassicaudata</i>	1	2	1
<i>P. gilesi</i>	1	—	—
<i>P. tenuirostris</i>	—	—	1
Captures/trap day	0.0103	0.0222	0.0067

TABLE 2. Captures of each species during Test B. Description of traps given in the next.

Species	Denim only	Denim with mesh back	Type of Trap Mesh back only	Standard Elliott	Drift fence
<i>S. macroura</i>	—	1	—	1	—
<i>P. gilesi</i>	7	1	1	6	3
<i>P. tenuirostris</i>	—	—	—	—	2
<i>M. musculus</i>	1	3	3	3	1
Total Captures	8	5	4	10	6
Captures/trap day	0.032	0.015	0.012	0.010	0.031

ARID ZONE MAMMAL CAPTURE TECHNIQUES

TABLE 3. Captures of each species during Test C. Drift line profiles as shown in Fig. 1.

Species	Drift line profile			Elliott traps
	(b)	(c)	(d)	
<i>S. crassicaudata</i>	—	1	1	1
<i>P. gilesi</i>	3	6	—	—
<i>P. tenuirostris</i>	3	3	3	—
<i>M. musculus</i>	—	—	—	5
Total Captures	6	10	4	6
Captures/trap day	0.0087	0.0145	0.0058	0.0015

that individuals followed fence profiles shown in Fig. 1, b and d. The high trap success for the fence of this profile (Table 3) supports these observations. A fence profile shown in Fig. 1, a is not very efficient and most *S. crassicaudata* individuals quickly turned away from it or followed it no more than 1-2 m.

These behavioural observations indicate that the success of pitfall trapping depends on the propensity of animals to follow the drift fence and associated with this, the trap spacing along the drift line. Spacing of pitfall traps at 10 m intervals is considered too great and spacing at 5-6 m intervals is more appropriate.

Captures in Elliott traps during Test B show marked differences between species (Table 2). No *P. tenuirostris* individual was caught in an Elliott trap but *P. gilesi* individuals had a preference for traps with denim floor coverings and a solid rear door. Those traps fitted with a mesh rear door were preferred by *M. musculus* individuals. Captures of *S. macroura* were too few to indicate trap preferences by this species. Elliott traps had variable success in trapping *P. gilesi* individuals (Tables 2 and 3) and, compared with pitfall traps they are an unreliable technique for this species.

It is worth commenting on the effectiveness of the two types of pit trap used. Some planigales gripped the rim of the metal pits and escaped without entering the pit, but the rounded rim of the plastic traps did not allow individuals that initial hold with the hind feet. Unfortunately the plastic traps soon became brittle, cracked and had to be discarded whereas the metal traps were not affected.

CONCLUSION

The choice of trapping technique and method in a given situation will ultimately depend on several factors which include: (i) the available resources of manpower and materials; (ii) the target species; (iii) the purpose for capturing that species, i.e. specimen collection, short term survey or long term study. For ecological studies of *P. gilesi* and *P. tenuirostris* such as Read (1984), a most effective technique was one of pitfall traps at 5-6 m intervals with a drift fence

of profile shown in Fig. 1, b. This was judged in terms of the number caught and the speed of operation. It was a compromise of trap response and available manpower.

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Biology and Habitat Usage of Sympatric Populations of the Fawn-footed Melomys (*Melomys cervinipes*) and the Grassland Melomys (*M. burtoni*) (Rodentia: Muridae)

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ABSTRACT

A mark-recapture study of small mammals was conducted in a swamp-forest association on Kinaba Island and adjacent mainland, Cooloola. Over 15,527 trap-nights and 9,891 trap-days, 34 individual male and 27 female *M. cervinipes* and 43 individual male and 31 female *M. burtoni* were trapped. *M. cervinipes* were found to breed from August to January, whilst there was no clear season for *M. burtoni* which bred throughout the year. Adult *M. cervinipes* and *M. burtoni* are noticeably different in size. *M. cervinipes* density increased over the study while that of *M. burtoni* decreased. A dry change in the environment was possibly responsible for these population dynamics. *M. cervinipes* and *M. burtoni* have different habitat requirements and so are typically segregated in space. Clear ecological and biological differences in the two species must help to alleviate competition between them.

INTRODUCTION

The Fawn-footed Melomys (*Melomys cervinipes*) is usually found in closed forest, but may also occur outside this habitat type (Watts and Aslin 1981). It has previously been recorded in coastal mangrove forests by Lavery and Johnson (1974). Populations have been studied by Wood (1971) and Freeland (1972) in sub-tropical rainforest, but in general capture data is sparse, and biology and population characteristics poorly known elsewhere (cf. Watts and Aslin 1981).

The Grassland Melomys (*M. burtoni*) is smaller than *M. cervinipes*. It typically inhabits tropical and sub-tropical grasslands, sedgeland and open forest or woodland with a grassy understorey (Watts and Aslin 1981). It has also been trapped in canefields of north Queensland (Gard 1935, McDougall 1944 and 1946, Redhead 1973). Comparatively little is known about the biology of the Grassland Melomys (Watts and Aslin 1981).

Melomys cervinipes and *M. burtoni* are known to be sympatric over parts of their range. In this study *M. cervinipes* and *M. burtoni* were trapped in a swamp-forest association on Kinaba Island in Lake Cootharaba and on the adjacent mainland in the Cooloola 'wallum' of southeastern Queensland (Coaldrake 1961). Hockings (1977), Dwyer, Hockings and Willmer (1979) and Dwyer, Kikkawa and Ingram (1979) have also trapped both species in the 'wallum' country. They found *M. cervinipes* to be most clearly associated with closed forest and *M. burtoni* most abundant in wet-heathland.

For Kinaba Island and nearby mainland, information on trapping success, breeding biology, weight, longevity, trappability, population density and structure,

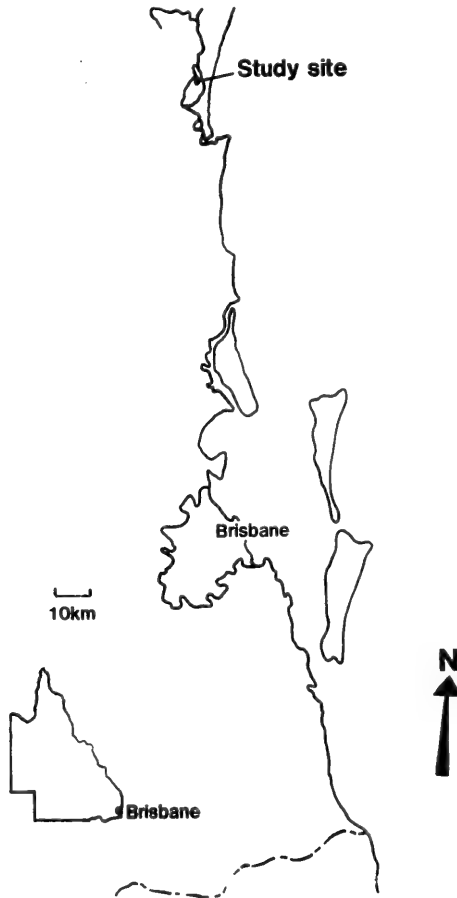


Fig. 1. Location of the study site.

SYMPATRIC POPULATIONS OF TWO *MELOMYS* SPECIES

home range, movements and utilization of space are given for both species. Trapping returns were low for both species.

STUDY AREA AND METHODS

The work described here was carried out at Kinaba Island and on the adjacent mainland (lat. 26°14'S, longit. 153°02'E; see Figs. 1 and 2). The island lies at the southern end of the Cooloola National Park. The region has been broadly described as 'wallum' (Coaldrake 1961). The island and adjacent mainland is dominated by the Swamp Oak (*Casuarina glauca*) and the Paperbark (*Melaleuca quinquenervia*), which both grow to 20 metres. A more detailed description of the study site has been given by Smith (1984) and of the Cooloola region by Dwyer, Hockings and Willmer (1979). The island undergoes infrequent inundation and it appears that it was formed by alluvial deposition.

Climatic conditions experienced at Kinaba Island and the whole of the Cooloola region were described by Smith (1984) and Dwyer, Hockings and Willmer (1979), respectively.

Melomys cervinipes and *M. burtoni* were trapped in Elliott traps (33 x 20 x 10 cm) and larger wire traps (40 x 15 x 20 and 52 x 20 x 25 cm). Trapping sessions were in May, mid-June, late July-early August and Mid-September, 1976, and monthly from January, 1977 to January, 1979.

In Fig. 2, Areas 1, 2 and 7A and 7B are the sites where trapping grids occurred. Grid lines and trap points in each line were 20 metres apart. The 'effective' sampling areas of these grids are taken to include a 10 metre boundary strip (where possible) around the outer margin of traps. Line transects were established in Areas 3, 4, 5 and

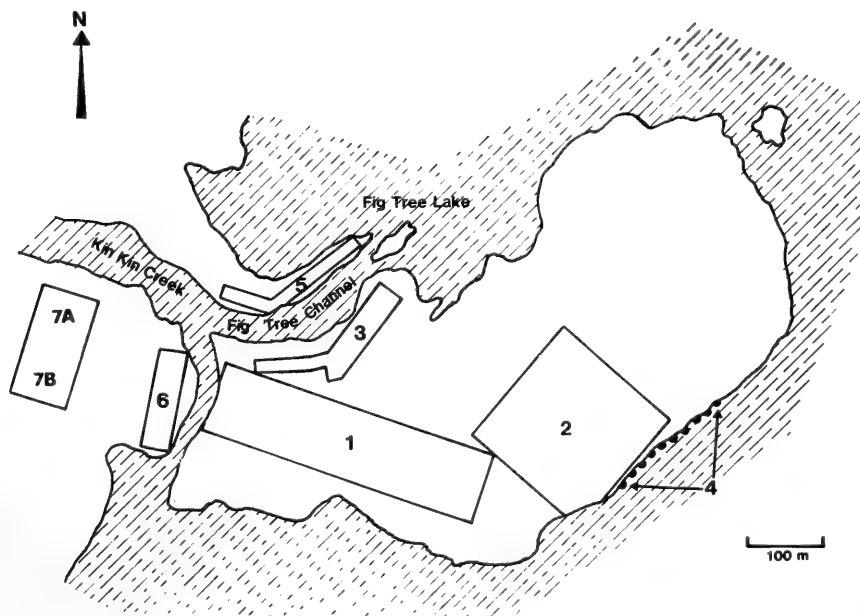


Fig. 2. Details of study area showing trapping areas.

6 (Fig. 2). Adjacent trap lines and trap-sites in lines were also 20 metres apart. The numbers of trap-sites in Areas 1, 2, 3, 4, 5, 6, 7A and 7B were 100; 97, 20, 10, 12, 14, 32 and 32 respectively. Areas 7A and 7B contained 16 trap-sites in common. One trap was placed at each site. Areas 3 and 4 were trapped in two and three sessions respectively. Areas 5 and 6 were established to monitor transfers from island to mainland and vice versa. In each area, traps were operated for between two to four consecutive nights in any one trapping period. Traps were left open but unbaited through the day. They were baited in the late afternoon with bacon and sweet potato soaked in vegetable oil and cleared the next morning.

On Kinaba Island traps were operated over 13,803 trap-nights and 8,887 trap-days. On the mainland, 1,724 trap-nights and 1,004 trap-days were logged.

At first capture, animals were individually marked by toe-clipping. At this time and at each recapture, the following information was recorded: For females (1) condition of the vagina (a) perforate or imperforate, (b) with or without sperm plug; (2) teat condition (a) small, medium, large or regressed (b) lactating on palpation or not lactating; (3) evidence of pregnancy, discerned by palpation. Palpation was only successful for later stage pregnancies. Undetected pregnancies were evidenced by teat enlargement during lactation. Reproductive condition of males was coded as: *Testes 1* (testes not descended into the scrotal sac), *Testes 2* (testes scrotal but small), *Testes 3* (Medium to large scrotal testes with an unenlarged cauda epididymal sac), *Testes 4* (Large scrotal testes with cauda epididymal sac enlarged), and *Testes 4-* (Testes that had previously been *Testes 4* but with the cauda epididymal sac collapsed). Breeding refers to the birth and nursing of young.

Known to be alive (KTBA) estimates of population size were used (Krebs 1966). Retrappability indices assess how easily animals are caught by the use of trapping techniques and these indices can be subsequently used to determine KTBA exclusion periods (see Hockings 1977). Average retrappability for *M. cervinipes*, both sexes combined, was 0.5 ($s = 0.42$, $n = 16$). The species is trap 'shy' (cf. Wood 1971, Hockings 1977; Fletcher 1978) and for this reason individuals were only excluded from KTBA estimates if absent for more than four trapping sessions. For *M. burtoni*, average retrappability for the island, both sexes combined, was 0.63 ($s = 0.33$, $n = 9$). Individuals were excluded from KTBA estimates if absent for greater than two trapping sessions. Retrappability for the mainland was lower ($\bar{x} = 0.43$, $s = 0.43$, $n = 17$) and thus individuals were only excluded from KTBA estimates if absent for greater than four trapping sessions. Differences in trappability between island and mainland are more likely to reflect inadequacies in the trapping programme than actual differences intrinsic to the populations.

Transients include those individuals caught either in one trapping period only, or in single periods separated by intervals greater than the KTBA inclusion period. Because transience may be correlated with the proportion of traps on the perimeter of a grid, the differently shaped grids may influence this measure. Indices of home range size were calculated using Brant's (1962) measure of average distance between successive captures (AvD measure). Distances between captures were measured within grids only and not between grids and lines.

RESULTS

TRAPPING SUCCESS

Thirty males and 27 females *M. cervinipes* were trapped on Kinaba Island a total of 215 times. The sex ratio was 1:1 ($X^2 = 0.07$, $df = 1$, $P > 0.05$). Four individual males were trapped a total of five times on the mainland. Capture rates for the island and mainland were 1.55% and 0.29% respectively.

SYMPATRIC POPULATIONS OF TWO MELOMYS SPECIES

Eleven *M. burtoni* females and 23 males were trapped on the island and this was significantly biased from 1:1 ($X^2 = 6.08$, $df = 1$, $P < 0.05$). These individuals were trapped 155 times, a capture rate of 1.2%. Three captures on the island were made during daylight hours (% capture rate = 0.03%). Twenty females and 20 males were captured a total of 98 times on the mainland, a capture rate of 6.12%.

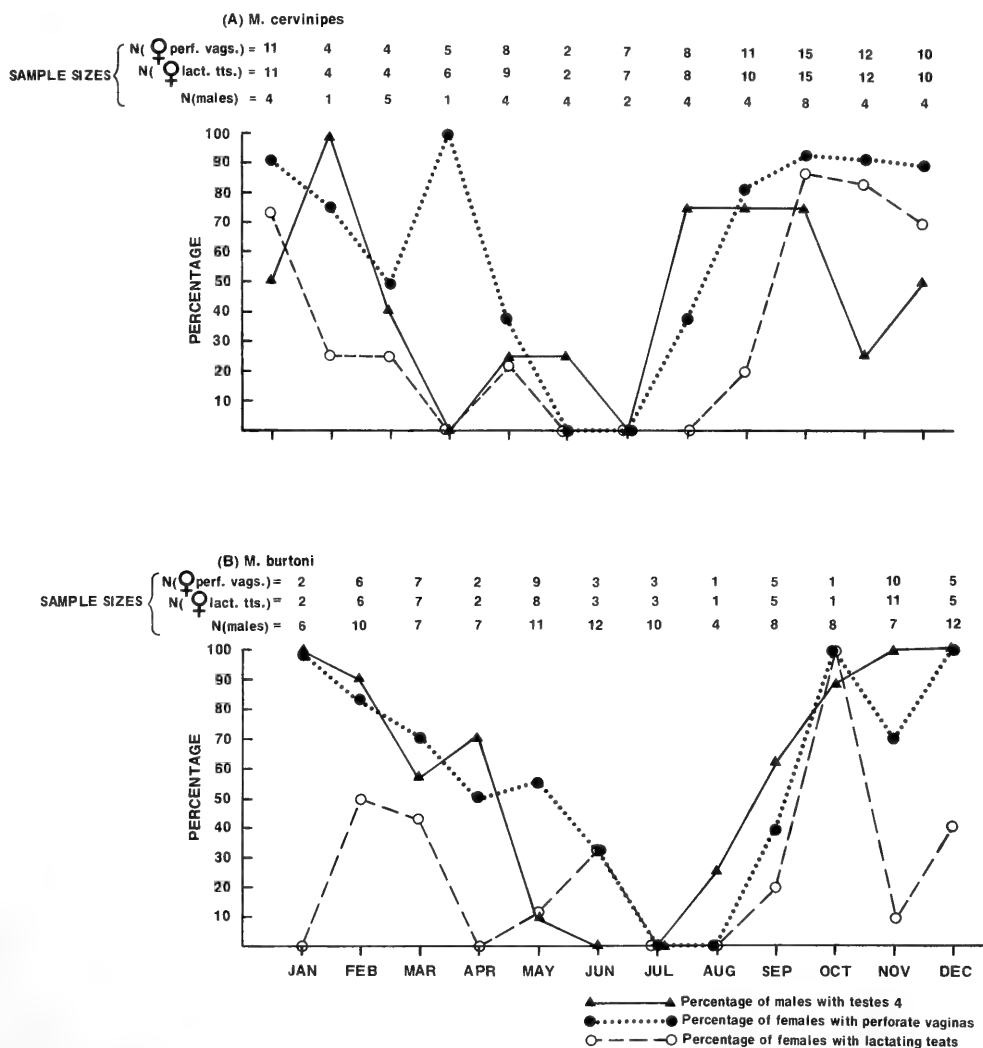


Fig. 3. Reproductive data for (A) *M. cervinipes* and (B) *M. burtoni*. Data pooled from all years.

BREEDING

Data relevant to determining breeding periods are given in Fig. 3 for both species.

M. cervinipes

Males with Testes 4 were uncommon (i.e. proportions ≤ 0.4) from March to July (i.e. autumn to winter). One adult male with regressed testes was trapped in May, 1978 and another in June, 1977.

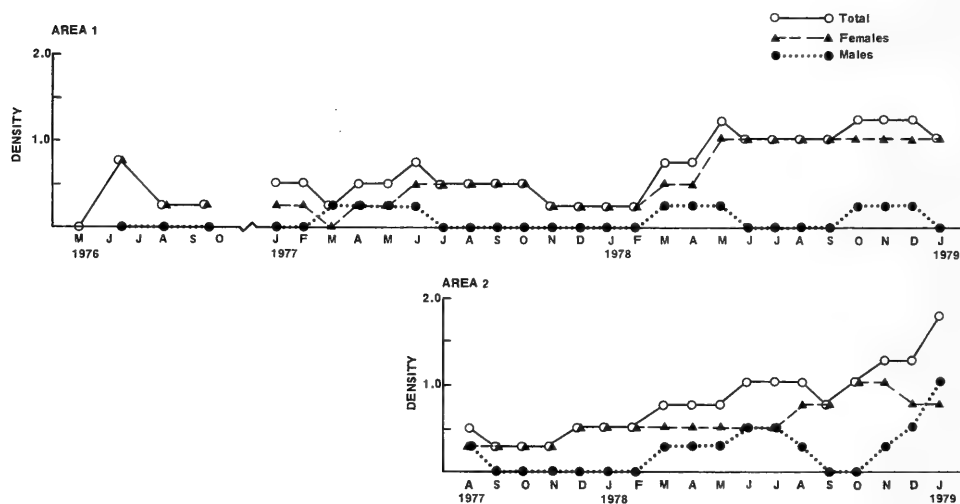


Fig. 4. Densities (residents/ha) of *M. cervinipes* from KTBA estimates in areas 1 and 2.

No females with perforate vaginas were trapped through the winter months of June or July. Five females that had previously been perforate became sealed between May and August. Two females with lactating teats were trapped in September, thus some mating activity that resulted in fertilisation must have occurred through the winter months (assuming a 38 day gestation period, Watts and Aslin 1981). Lactating females were most commonly encountered between October and January (i.e. spring to mid-summer).

The data for males and females combined seem to suggest that most successful mating encounters and subsequent breeding activity occurs between August and January and that occurrences outside this period are rare.

A maximum of two litters per female in a breeding season was recorded, although the average rate of pregnancy per female per season was 1.3 ($s = 0.77$, $n = 18$).

SYMPATRIC POPULATIONS OF TWO *MELOMYS* SPECIES

M. burtoni

Evidence of breeding on Kinaba Island came from Area 4 only. A pregnant female was trapped in November, 1978 and two females with lactating teats were trapped in December, 1978. Males with Testes 4 and females with perforate vaginas were recorded from Areas 1, 2 and 4. Evidence of breeding was noted in all mainland areas.

Males with Testes 4 were trapped in all months except June and July. Some regression of testes occurred in these months, as well as in May, August and October.

Lactating females were caught in all months other than January, April, July and August. The proportions of females with perforate vaginas were at a minimum in June and July.

In general, breeding activity appears to decline during the cooler months, but no main breeding season was identified.

WEIGHTS AND LONGEVITY

M. cervinipes

Male *M. cervinipes* attained adult weights ranging between 61g and 102g (\bar{x} = 83.1, s = 10.96, n = 29) and females (pregnant females included weights between 55g and 115g (\bar{x} = 73.2, s = 11.62, n = 113). The lightest male trapped weighed 18g and the lightest female 17g. Both these individuals were trapped in October 1978 and had probably recently been weaned.

A male that was trapped over 16 months after its sexual maturation at four to six months (Freeland 1972) was estimated to have been approximately 21 months at last capture. A female that was first captured as an adult was trapped over 17 subsequent months. Its age when last trapped must have been at least 23 months.

M. burtoni

Male *M. burtoni* grew to weights that ranged between 47g and 67g (\bar{x} = 56.5, s = 5.16, n = 100) and females (pregnant females included) 26g to 58g (\bar{x} = 42.9, s = 7.09, n = 51). The lightest juvenile male caught weighed 23g and the lightest female 12g. P. Dwyer (pers comm.) has recorded 11g juveniles attached to teats, thus the latter individual was probably recently weaned.

POPULATION CHARACTERISTICS

M. cervinipes

Population densities of residents for Areas 1 and 2 are graphed in Fig. 4. Numbers of individuals caught in each trapping period are given in Table 1. No regular pattern in population fluctuations emerged. The increase in density in 1978 compared with the other years was due to an influx of mainly subadult

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TABLE 1. Total number of individuals (including transients) caught in each trapping session.

		<i>M. cervinipes</i>		<i>M. burtoni</i>			
Trapping Period		Area 1	Area 2	Area 1	Area 2	Area 6	Area 7A Area 7B
May	1976	0		5			
mid-June		4		6			
August		1		1			
mid-Sep.		1		0			
Jan.	1977	2		2			
Feb.		2		4		1	
March		2		2		2	
April		1		1			0
May		3		2		2	
June		3		1		2	7
July		1		1		0	8
August		1	2	0	2	0	
Sep.		2	1	1	0	1	8
Oct.		5	1	0	1	1	
Nov.		3	2	0	1		10
Dec.		1	2	1	3	1	
Jan.	1978	1	2	1	2	1	2
Feb.		0	3	0	5	1	
March		4	3	3	2		3
April		2	4	3	4		
May		7	1	2	1		6
June		0	2	1	2		
July		3	3	1	2		0
August		1	6	0	1		
Sep.		6	4	0	2		1
Oct.		7	9	1	3		0
Nov.		6	5	0	1		2
Dec.		5	6	0	1		2
Jan.	1979	4	7	0	0		0

individuals that were probably born during the spring to early summer period of 1977-78. The maximum density recorded (including transients) was 2.32 individuals per hectare in October 1978.

M. burtoni

Density estimates based on KTBA estimates are given in Fig. 5. Total numbers of individuals caught per trapping period are given in Table 1. The pattern of population fluctuation in Area 1 was regular from year to year. Evidently, individuals resided only temporarily in Area 1 during the summer months. Males made up a large proportion of the individuals in this area.

Compared with Area 1, population fluctuations in Area 2 did not show comparable trends. Numbers, which consisted principally of males, remained constant.

SYMPATRIC POPULATIONS OF TWO *MELOMYS* SPECIES

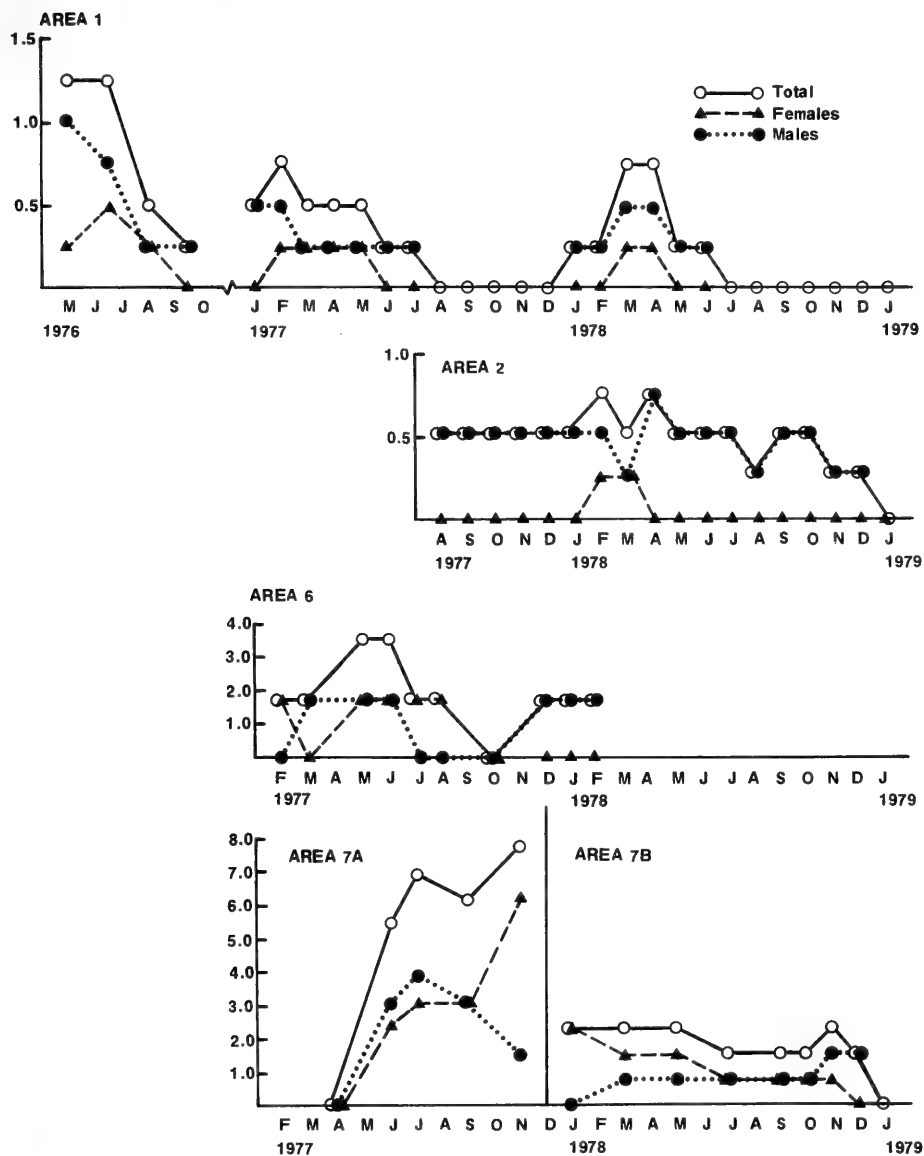


Fig. 5. Densities (residents/ha) of *M. burtoni* from KTBA estimates. Areas 1 and 2 = Kinaba Island. Areas 6, 7A and 7B = mainland.

On the mainland, no temporal trends in abundance for any area were evident. Nor was there similarity with island trapping areas. There was evidence that population numbers peaked prior to winter but declined during the ensuing cold months.

There was a decrease in the density of *M. burtoni* on Areas 1, 2 and 7B towards the end of the study. The highest densities recorded for the island and mainland were 1.51 and 7.81 individuals per hectare, respectively.

TRANSIENCE AND HOME RANGE

M. cervinipes

The numbers of individuals classified as transients and as residents for Areas 1 and 2 are given in Table 2. Transients were more common than residents in Area 1, but equally as common in Area 2. The high transient estimates reflect difficulties experienced in trapping the species.

Home ranges both within and between sexes overlapped. Male movements ($AvD = 71.52$ metres, $s = 35.50$, $n = 7$) were significantly greater than those of females ($AvD = 46.16$ metres, $s = 14.66$, $n = 14$) (Mann Whitney $U = 19$, $n_1 = 7$, $n_2 = 14$, $P < 0.05$). One female first captured on the mainland as a subadult was subsequently recaptured 14 months later on the island.

M. burtoni

The numbers of individuals classified as transients and as residents are given in Table 2. In Area 7A residents were more abundant than transients, but in all other areas the ratio of transients to residents was 1:1.

TABLE 2. Numbers of individuals classified as transients and as residents for *M. cervinipes* in Areas 1 and 2, and for *M. burtoni* in Areas 1, 2, 7A and 7B. Results of X^2 analyses testing for bias from a 1:1 ratio are given. Expected values in parentheses.

<i>M. cervinipes</i>			
	Transients	Residents	X^2 analyses
Area 1	24 (17.5)	11 (17.5)	$X^2_{adj} = 4.11$, $df = 1$, $P < 0.05$
Area 2	10 (9)	8 (9)	$X^2_{adj} = 0.06$, $df = 1$, $P < 0.05$
<i>M. burtoni</i>			
	Transients	Residents	X^2 analyses
Area 1	8 (9.5)	11 (9.5)	$X^2_{adj} = 0.21$, $df = 1$, $P > 0.05$
Area 2	6 (6)	6 (6)	—
Area 7A	2 (6)	10 (6)	$X^2_{adj} = 4.08$, $df = 1$, $P < 0.05$
Area 7B	4 (4)	4 (4)	—

SYMPATRIC POPULATIONS OF TWO *MELOMYS* SPECIES

The AvD measure of 73.94 metres ($s = 52.37$, $n = 12$) calculated from island grid captures, males only, is likely to be an underestimate. Several records of dispersion across water barriers were made. Two individual males crossed the channels separating island and mainland at least twice each. Females also were rafted or swam across the channels.

RESOURCE UTILIZATION

Capture data for *M. cervinipes* and *M. burtoni* at each trap station were tested in pair-wise combination using Spearman Rank Correlation analysis. In Area 1 no relationship was evident ($r_s = -0.1139$, $t = -1.135$, $df = 98$), but in Area 2 captures were negatively correlated ($r_s = -0.3051$, $t = -3.123$, $df = 95$). Either mutual exclusion occurred between species or they preferred different vegetation types. This has not been tested here.

All captures of breeding *M. burtoni* females occurred in the two trapping lines adjacent to the island edge in Area 2; in Area 4; and in Areas 5, 6, and 7A of the mainland.

DISCUSSION

BREEDING

If breeding activity of *M. cervinipes* is restricted to between the months of August and January as the data suggest, then the main breeding season is relatively short compared to populations in rainforest at Mt Glorious, southeastern Queensland (cf. Wood 1971, Freeland 1972). Some females produced more than one litter per year and this is not uncommon for *M. cervinipes* (cf. Taylor and Horner 1970, Freeland 1972).

At Kinaba Island and in the adjacent mainland, no obvious breeding season was evident for *M. burtoni*. In other localities at Cooloola parturition occurs mainly between September and March, although some winter breeding activity is evident (Hockings 1977). McDougall (1946) found that this species breeds mainly in autumn and winter in north Queensland. Breeding females were found on the island perimeter and in mainland areas only, where the habitat consisted of dense stands of restiads, grasses and/or reeds in or near to permanent water. In this type of environment females are probably able to find suitable places to build nests (Gard 1935).

It seems that the breeding seasons of *M. cervinipes* and *M. burtoni* overlap considerably, but that the localities of nests are probably quite different. Such differences would alleviate any possible competition for nest space.

WEIGHT

Within sex, adult *M. cervinipes* are typically heavier than *M. burtoni*, although there is a small overlap in the weight ranges (cf. Watts and Aslin 1981).

POPULATION PHENOMENA

Poor trapping success of *M. cervinipes* stems from the inadequacy of traps placed on the ground for capturing this partly arboreal species. Hockings (1977), Barry (1977) and Dwyer, Hockings and Willmer (1979) noted that in areas where overhead runways were abundant, trapping returns probably led to underestimates of true densities within these habitats. The maximum recorded density of 1.8 individuals per hectare is less than half that noted for blackbutt-*Banksia aemula* forest near Ramsay's rainforest, Cooloola (cf. Dwyer, Hockings and Willmer 1979).

Variability in *M. burtoni* density and population dynamics between areas suggest differential usage of habitats. Animals of this species appear to prefer dense vegetation (Hockings 1977, pers obs). During periods through which space may be at a premium in these favoured areas, individuals may find it necessary to overflow into adjacent, suboptimal habitats. In late summer and winter, peripheral habitat was occupied by mostly males. The maximum density recorded in Area 7A on the mainland, is the highest yet known for the Cooloola region (cf. Dwyer, Hockings and Willmer 1979). This is not surprising considering that this wetland with dense vegetation at the shrub and herb levels is ideal habitat for *M. burtoni* (Hockings 1977, Watts and Aslin 1981).

Over the period of the study the densities of *M. burtoni* decreased on Areas 1 and 2 whilst *M. cervinipes* numbers increased. This is believed to be a response to low rainfall experienced late in the study which led to dry conditions, rendering the environment more suitable to occupation by *M. cervinipes* than *M. burtoni*.

HABITAT USAGE

M. cervinipes is adapted to an arboreal existence (Wood 1971, Freeland 1972, Fletcher 1978, pers obs). The tail is prehensile and on release animals frequently climbed a nearby tree or vine with considerable skill. *M. burtoni* also has a prehensile tail but its climbing is probably restricted to tall reeds and sedges (Watts and Aslin 1981) where it feeds. No *M. burtoni* climbed a tree or vine upon release. It would appear that although *M. cervinipes* and *M. burtoni* populations share a swamp-forest habitat on an island in the 'wallum' of southeastern Queensland, they segregate at a finer scale within this habitat.

ACKNOWLEDGEMENTS

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A Creel Survey of the Lake Keepit Recreational Fishery

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ABSTRACT

A creel survey was conducted at Lake Keepit, N.S.W., on 48 days from October, 1981 through September, 1982. A total of 1285 counts of shore and boat anglers were made and 1236 anglers were interviewed. Estimated total fishing effort and catch during the period was 97,592 angler hours and 44,580 fish, respectively. Fishing effort was highest in spring and lowest in winter. Fishing effort decreased with falling water level. Angler success was highest in spring and late autumn. Five species of fish were caught, with Golden Perch (*Macquaria ambigua*, 94%) and Australian Catfish (*Tandanus tandanus*, 5%) dominating the catch. The mean weight of caught Golden Perch was 1.2kg and Australian Catfish 1.0kg. The evidence indicates that Lake Keepit supports an excellent recreational fishery.

INTRODUCTION

Lake Keepit is one of the most popular inland fishing locations in NSW (Smith 1983, Wilson 1983). The resident warmwater fish populations include those of the popular angling species Golden Perch (*Macquaria ambigua*), Australian Catfish (*Tandanus tandanus*) and Murray Cod (*Maccullochella peelii*). There is no stocking of hatchery bred fish.

This creel survey was conducted in order to determine the magnitude of fishing effort, the size of the fish catch and other aspects of the recreational fishery. It forms part of a larger study of the upper Namoi River investigating possible adverse effects on the fish resources caused by the construction of the new Split Rock dam, above Lake Keepit.

STUDY AREA

The lake is located on the Namoi River just above its confluence with the Peel River, about 370 km north of Sydney and 50 km from Tamworth (population 30,000). It is an artificial storage which began filling in 1960. Its main purpose is to provide water for irrigation to the lower Namoi Valley. At full capacity the lake covers some 4,200 ha with a shoreline of 104 km, a maximum depth of 41 m and a capacity of 423,000 ML (Water Resources Commission, pers. comm.).

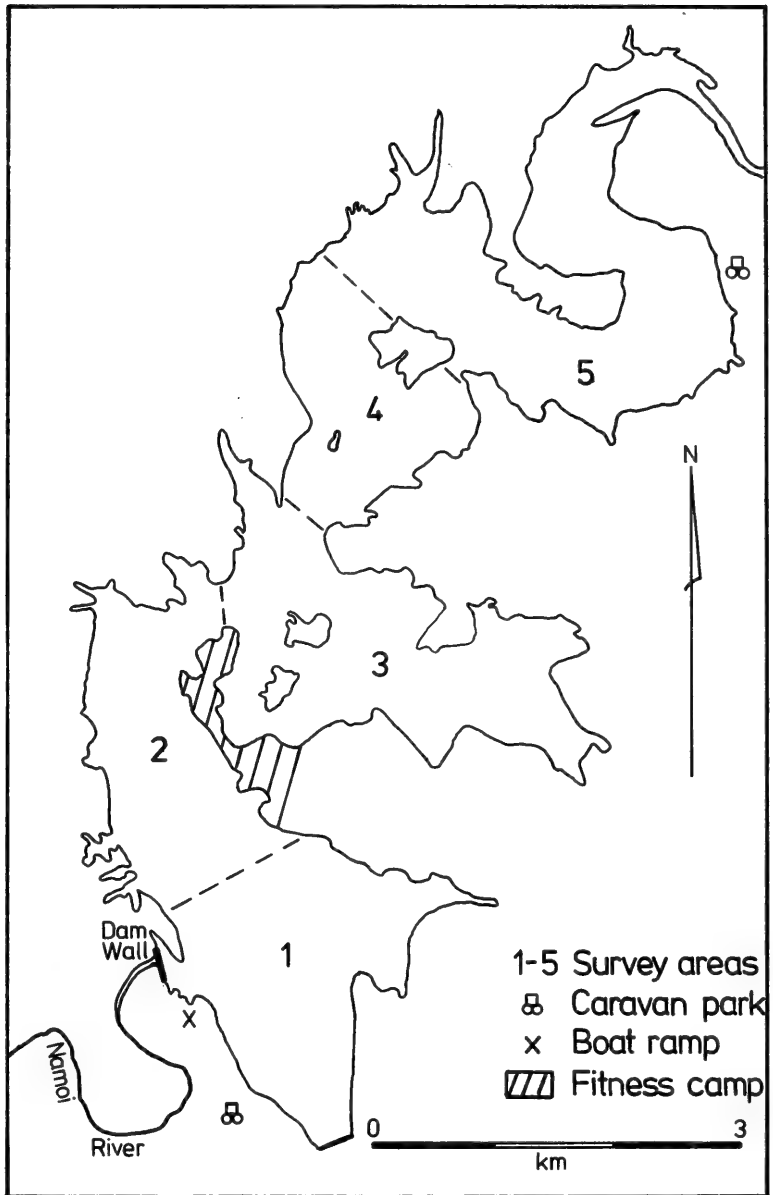


Fig. 1. Lake Keepit.

LAKE KEEPIT CREEL SURVEY

Historically the water level in Lake Keepit has fluctuated between 6 and 100% of maximum capacity since filling commenced in 1960. During this study the average water level was 28% of maximum capacity (a surface area of 1,630 ha), with a range of 44% (2,300 ha) in November 1981 to 15% (920 ha) in March 1982. The lake has fallen to the lower level encountered during this study only once previously, during the period 1966-68. The water volume of the dam is frequently above 70% capacity.

METHODS

For the purposes of this study Lake Keepit was divided into five areas (Fig. 1). Surveys were conducted from a boat and consisted of angler counts and interviews. The surveys were carried out at monthly intervals commencing in October 1981 and concluding in September 1982 for a total of 48 days. The survey period for each month was two weekdays (usually Friday and Monday) and a weekend.

Headcounts involved driving a boat over the length of the lake and counting the anglers in each area, with the aid of binoculars. In this manner it was possible to complete a count of the five areas in approximately one hour with each count being considered instantaneous for that hour. Manpower and fuel constraints limited the number of counts from 4 to 8 per area per day depending upon weather conditions, boat operations and hours of daylight.

Anglers were randomly selected for interview during and between hourly counts of each area. An attempt was made to interview a minimum of 25% of the anglers in each area but this was not accomplished when the number of anglers in an area exceeded 50. The maximum number of interviews conducted each day did not exceed 20.

The relative proportion of each species caught in each monthly sample was determined. An estimate of the number of each species caught was calculated by multiplying the relative proportion of each species in the catch by the total estimated fish catch for each month.

Each month a random subsample of caught fish was measured and length-frequency histograms prepared.

Definitions of fishing effort, catch per unit effort and yield and their calculations follow Lambou (1966). Yearly calculations involving surface area use the average total surface area of 1630 ha which occurred during the survey period.

FISHING EFFORT

Fishing effort (P) is defined as the amount of fishing occurring on the lake during a specified period, measured in angler hours. Estimates of fishing effort were obtained from analysis of headcount data. Weekend and weekday fishing effort were calculated separately.

Fishing effort (P) in any area (a) during any month (i) was calculated using the following formula:

$$P_{ai} = (F_{ai})(h_i)(d_i) + (F_{ai})(h_i)(d_i)$$

where:

f_{ai} is the mean number of anglers per hour in area (a) for month (i), for a weekday.

F_{ai} is the mean number of anglers per hour in area (a) for month (i), for a weekend day.

h_i equals the hours of survey daylight for month (i).

d_i equals the number of weekdays in month (i).

D_i equals the number of weekend days in month (i).

CATCH PER UNIT EFFORT (CPUE)

CPUE is defined as the number or weight of retained edible fish caught per angler per hour. In this report edible fish are defined as Golden Perch, Murray Cod and Australian Catfish. The monthly CPUE's for shore and boat fisherman were calculated separately. A monthly combined CPUE was calculated using the following formula:

$$\text{Combined CPUE} = [(\text{Shore fisherman CPUE}) (\% \text{ shore fisherman}) + (\text{Boat fisherman CPUE}) (\% \text{ boat fisherman})] [100^{-1}].$$

YIELD

Yield or total edible catch is defined as the number or weight of fish harvested within a given period. An estimate of monthly yield was obtained by multiplying the monthly fishing effort by the monthly combined CPUE.

RESULTS

A total of 1,285 headcounts of anglers was recorded (Table 1). The total number of interviews conducted was 466. Interview data are set out in Table 2. Boat anglers comprised 64% of the interviews and shore anglers 36%. The mean monthly time spent fishing (the time the interviewed fishermen had already spent fishing) was 6.6 ± 4.2 SD hrs for shore anglers and 3.4 ± 2.3 SD hrs for boat anglers. The mean monthly expected duration of a fishing trip (the time the interviewed anglers expected to spend fishing) was 11.1 ± 3.5 SD hrs for shore anglers and 6.7 ± 3.5 SD hrs for boat anglers (Table 2). A monthly or seasonal pattern in the duration of fishing trips was not apparent for shore or boat anglers.

TABLE 1. Distribution of anglers at Lake Keepit.

Month	No. of Headcounts	Boat Anglers	Shore Anglers	Total	χ^2 (p=0.05)
October 1981	95	1425 (73.9)	503 (26.1)	1928	*
November 1981	117	1111 (82.7)	232 (17.3)	1343	*
December 1981	80	159 (78.3)	44 (21.7)	203	*
January 1982	90	378 (78.6)	103 (21.4)	481	*
February 1982	100	204 (54.3)	172 (45.7)	376	ns
March 1982	112	94 (34.4)	179 (65.6)	273	*
April 1982	138	278 (49.4)	285 (50.6)	563	ns
May 1982	137	339 (50.4)	334 (49.6)	673	ns
June 1982	119	147 (56.1)	115 (43.9)	262	ns
July 1982	105	34 (29.6)	81 (70.4)	115	*
August 1982	90	24 (42.1)	33 (57.9)	57	ns
September 1982	102	188 (60.8)	121 (39.2)	309	*
	1285	4381 (66.6)	2202 (33.4)	6583	*

No. of observed anglers during headcounts (percentages in brackets). * Significant difference between numbers of shore and boat anglers. ns: no significant difference.

LAKE KEEPIT CREEL SURVEY

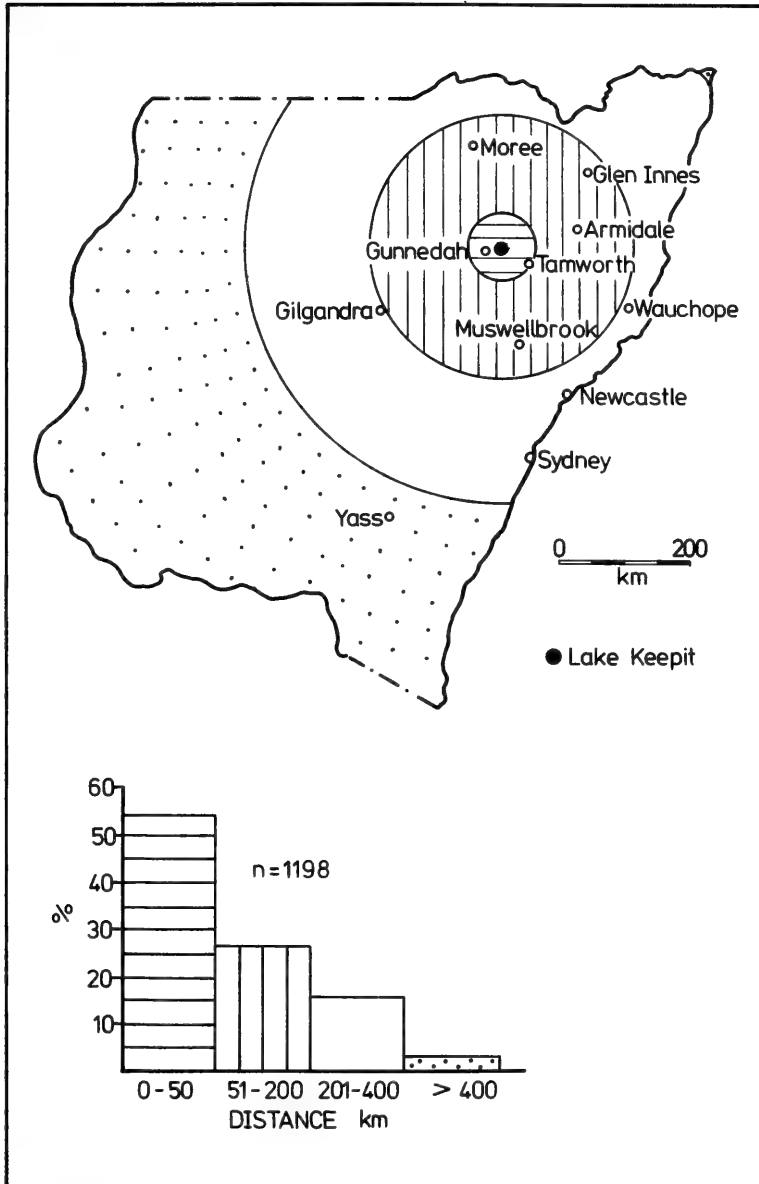


Fig. 2. Distribution of distances travelled by anglers to Lake Keepit, not including 38 anglers of unknown address.

TABLE 2. Creel survey data obtained from interviews.

Month	Year	Number of interviews	Number anglers interviewed	Number shore anglers	Number boat anglers	¹ Mean time spent (hrs)		² Mean expected duration of trip (hrs)		Night fishing estimate (as a percentage of day effort)
						Shore anglers	Boat anglers	Shore anglers	Boat anglers	
October	81	61	147	62	85	3.65	3.45	9.34	8.99	33
November	81	42	117	15	102	7.68	2.82	14.91	7.32	29
December	81	24	72	19	53	6.46	2.72	10.00	4.00	5
January	82	53	147	21	126	17.45	1.76	18.47	3.80	22
February	82	49	133	43	90	4.64	2.04	8.80	5.22	25
March	82	31	85	46	39	4.76	4.58	8.67	7.14	24
April	82	54	162	70	92	3.46	2.07	8.48	4.15	23
May	82	61	145	68	77	2.14	2.64	8.90	4.32	31
June	82	33	82	35	47	5.70	2.95	10.58	4.65	30
July	82	18	39	21	18	9.92	2.48	16.46	4.33	37
August	82	8	20	11	9	9.39	10.34	10.27	12.11	28
September	82	32	87	35	52	3.47	3.09	8.43	14.44	37
TOTAL		446	446	446	790					

1. The actual time spent fishing when interviewed for each angler per month 2. Trip = fishing session per angler.

Over 50% of the anglers travelled less than 50 km to the lake (Fig. 2). Some 36% came from Tamworth, 13% from Gunnedah and 4% from Manilla. Fishing club members made up 30% of the anglers.

FISHING METHODS

More anglers fished from boats (66.6%) than from the shore (33.3%) (Table 1). A monthly pattern was apparent with significantly more anglers fishing from boats than from the shore during the period September to January (Table 1). March and July were the only months in which the number of shore anglers significantly exceeded boat anglers (Table 1).

Several baits were used with worms, shrimps and yabbies most favoured (Table 3). Both handlines and rods were used with a mean of 2.2 fishing lines per person.

FISHING EFFORT AND AREAS FISHED

The monthly fishing effort was highest during the spring and decreased during summer and autumn to reach a low during winter (Fig. 3). The estimated annual fishing effort was 97,592 angler hours (a.h.) representing an average angler effort of 267 angler hours day (a.h./d.) ranging from 1,074 a.h./d. in October to 29 a.h./d. in August. As the average surface area for the year was 1,630 ha, this corresponds to an annual angling effort of 60 a.h./ha. Since the mean duration of a fishing trip per angler was 8.3 hrs (Table 2), an estimated 12,000 angler trips to

LAKE KEEPIT CREEL SURVEY

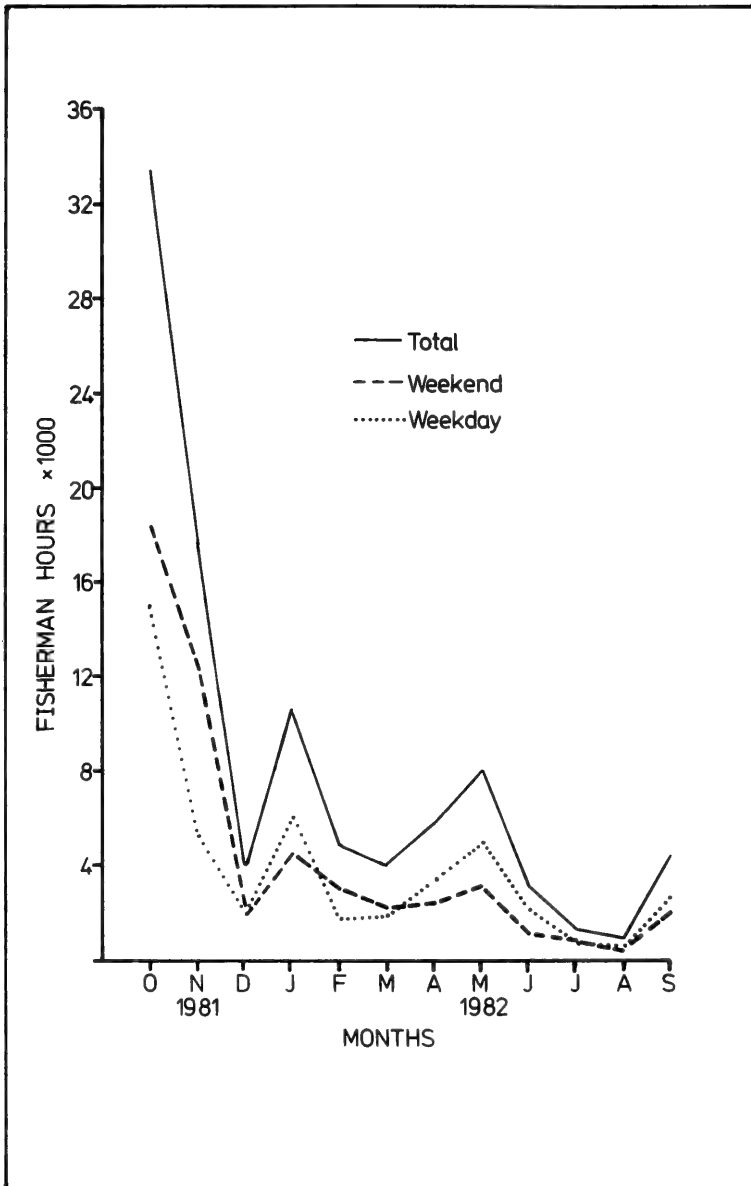


Fig. 3. Monthly fishing effort.

TABLE 3 Composition of bait.

Month	Worms	Shrimp	Yabbies	Prawns	Grubs	Lures	Others	No. of interviews
October 81	37(61)	29(48)	29(48)	6(10)	3(5)	1(2)	1(2)	61
November 81	11(26)	27(64)	20(48)	6(14)	—	—	—	42
December 81	12(50)	15(63)	7(29)	7(29)	—	—	—	24
January 82	15(28)	45(85)	10(19)	1(2)	—	2(4)	1(2)	53
February 82	21(43)	31(63)	15(31)	4(8)	—	1(2)	1(2)	49
March 82	20(65)	19(61)	8(26)	4(13)	—	—	1(3)	31
April 82	36(67)	35(65)	12(22)	8(15)	3(6)	—	2(4)	54
May 82	30(49)	43(70)	12(20)	2(3)	—	2(3)	1(2)	61
June 82	15(54)	25(76)	4(12)	1(3)	1(3)	1(3)	—	33
July 82	13(72)	8(44)	2(11)	1(6)	2(11)	1(6)	—	18
August 82	5(77)	4(57)	1(14)	3(43)	—	1(14)	—	7
September 82	16(50)	17(53)	14(44)	—	3(9)	—	—	32
TOTAL	231(50)	298(64)	134(29)	43(9)	12(3)	9(2)	7(2)	465

Number of interviewed parties using various baits (% in brackets). N.B. A party may use several types of bait hence percentages may exceed 100%

Lake Keepit occurred. Angling effort was positively correlated to lake level ($r=0.60$, $p<0.05$) and CPUE ($r=0.63$, $p<0.05$) (Table 4). Some 34% of the annual fishing effort occurred in October 1981 (lake level 37%). The period October 1981 to January 1982 accounted for 66.7% of the annual angling effort. It is assumed this was partly in response to a high CPUE and school holidays. Smaller peaks in angling effort occurred in the school holiday periods of May and September 1982 (Fig. 3). The interviews revealed that many anglers fished at dusk and the amount of fishing during darkness hours was estimated at 27% of the day time effort (Table 2). However, as these estimates were

TABLE 4. Monthly fishing effort and lake level.

Month	Fishing effort	Lake level (%)
October 1981	33,307	37
November	17,552	43
December	4,058	42
January 1982	10,479	31
February	4,763	20
March	3,956	15
April	5,734	25
May	7,944	25
June	3,156	25
July	1,372	20
August	906	22
September	4,365	21

LAKE KEEPIT CREEL SURVEY

from interview data and not confirmed by visual counts they were not included in the annual fishing effort estimates. Fishing effort over the year was greater on weekends (53%) than on weekdays (Fig. 3).

CATCH COMPOSITION

Five species of fish were caught by anglers with Golden Perch, Australian Catfish and Murray Cod representing 100% of the retained edible catch. The other species caught, European Carp (*Cyprinus carpio*) and goldfish (*Carassius auratus*) constituted a small percentage of the total catch (Table 5) but were not retained for consumption. Additionally, Silver Perch (*Bidyanus bidyanus*) are caught in the lake (Hawker pers. comm.), although none were observed in the survey. Overall, Golden Perch represented 94.1% of the catch (94.6% of edible catch) and Australian Catfish 5.3% (Table 5). The average length of Australian Catfish caught was 457 ± 75 SD mm and of Golden Perch was 420 ± 45 SD mm (Fig. 4). With the exception of one small Golden Perch (total length 280 mm) no fish were returned to the lake by anglers.

FISH CATCH AND CATCH PER UNIT EFFORT (CPUE)

The estimated yield from Lake Keepit from October 1981 to September 1982 was 44,580 fish. This represents an average of 122 fish/day, ranging from 579 fish/day in November 1981 to 1 fish/day in August 1982 (Table 5).

The mean monthly CPUE for shore anglers was 0.20 ± 0.27 SD fish/a.h. and for boat anglers 0.32 ± 0.27 SD fish/a.h. The mean monthly CPUE for shore and boat anglers combined, was 0.29 ± 0.26 SD fish/a.h., (Table 5).

TABLE 5 Catch statistics and catch composition.

Month	Year	Combined CPUE (fish/angler hour)	Catch (no fish)	Catch composition (% of monthly catch)									
				Golden perch		Australian Catfish		Murray cod		European carp		Goldfish	
				%	No.	%	No.	%	No.	%	No.	%	No.
October	81	0.50	16,654	100.0	16,654	0.0	0	0.0	0	0.0	0	0.0	0
November	81	0.99	17,376	100.0	17,376	0.0	0	0.0	0	0.0	0	0.0	0
December	81	0.36	1,461	97.4	1,423	2.6	38	0.0	0	0.0	0	0.0	0
January	82	0.32	3,353	85.5	2,867	14.5	486	0.0	0	0.0	0	0.0	0
February	82	0.18	857	53.7	460	44.9	385	0.0	0	1.4	12	0.0	0
March	82	0.17	673	7.5	50	83.8	565	0.0	0	7.5	50	1.2	8
April	82	0.08	459	59.5	273	23.8	109	0.0	0	16.7	77	0.0	0
May	82	0.20	1,589	70.7	1,123	25.3	402	0.0	0	4.0	64	0.0	0
June	82	0.31	978	97.2	951	1.9	18	0.0	0	0.9	9	0.0	0
July	82	0.07	96	100.0	96	0.0	0	0.0	0	0.0	0	0.0	0
August	82	0.04	36	88.9	32	11.1	4	0.0	0	0.0	0	0.0	0
September	82	0.24	1,048	60.6	635	32.4	340	2.8	29	4.2	44	0.0	0
TOTAL		$\bar{X} = 0.29$	44,580		41,940		2,347		29		256		8

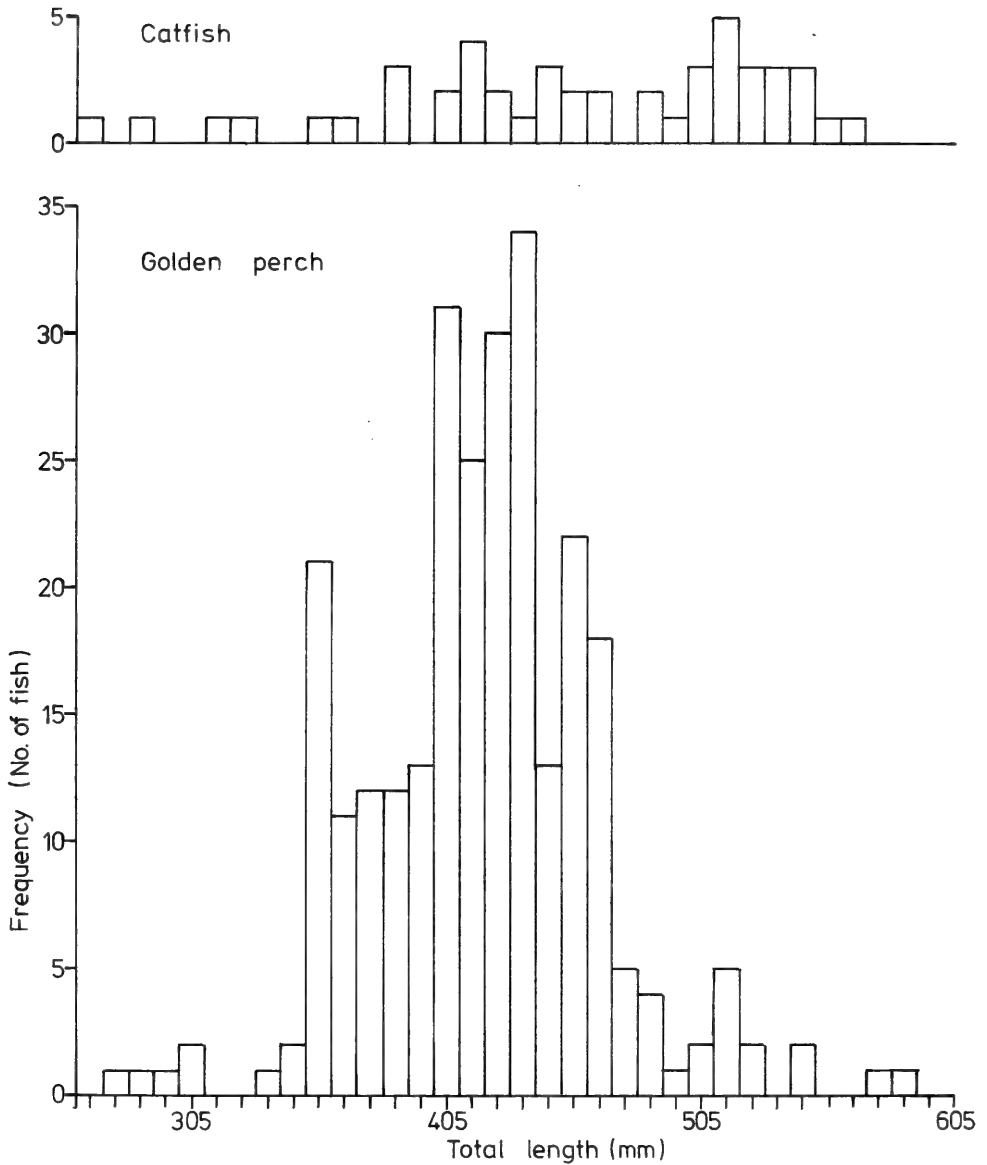


Fig. 4. Length frequency histograms for Australian Catfish (457 ± 75 mm, $n = 47$) and for Golden Perch (420 ± 45 mm, $n = 273$).

LAKE KEEPIT CREEL SURVEY

The mean weight of each fish caught was 1.2 kg (Golden Perch 1.2 kg, catfish 1.0 kg). The average weight of fish caught per hour by anglers was 0.35 kg. The estimated weight of total catch was 52,236 kg at a mean yield of 32.0 kg/ha.

DISCUSSION

Little creel survey data exist for freshwater impoundments within Australia and they are concerned with coldwater salmonid fisheries (Batho 1982). These fisheries are subject to closed seasons, minimum legal fish sizes and bag limits, and cannot be compared directly with the Lake Keepit fishery which has no such restrictions.

Fishing effort at Lake Keepit (60 a.hrs/ha/yr) is very similar to that of overseas warm freshwater fisheries (Jessop 1980, Von Geldern 1972). In Australia, Virgona (1984), SPCC (1981), Henry and Virgona (1980) and Tilzey (1978) reported fishing efforts of 68, 65, 63 and 59 a.h./ha/yr, respectively. However, fishing efforts of as high as 670 a.h./ha/yr (Dredge 1978) and 167 a.h./ha/yr (Henry 1984) and as low as 37 a.h./ha/yr (Pepperell 1980) and 5 a.h./ha/yr (Beinssen 1978) have been recorded.

The fishing effort at Lake Keepit was positively correlated to CPUE and lake level. These two factors appear partly responsible for the peak in fishing effort during October and November. In fact this peak was the dominant feature of fishing effort estimates for the entire year. CPUE was correlated to lake level ($r=0.79$, $p\ 0.05$) and was probably an important factor influencing fishing effort. Another important influence on CPUE is probably the reproductive cycling of the fish. Golden Perch spawning migrations were present in the lake and its feeder streams during October and November (unpublished data) and although feeding activity is low in migrating fish (unpublished data) increased CPUE may be related to post spawning activity. The decline in angler effort during December can be attributed in part to adverse weather conditions on survey days and the alternative demands placed on leisure time in the period prior to Christmas. While the response of anglers to weather was not analysed it is likely to have been an important factor. According to Malvestuto *et. al.* (1979), anglers are primarily influenced by climatic conditions either directly, for example, through unpleasant weather for recreational activities, or indirectly, through effects on fish behaviour (i.e. catchability).

It is likely that lake level fluctuations affect fishing effort from year to year in Lake Keepit. Many anglers stated that fishing was better when the lake level was higher and indicated that they fished more at such times. In other studies of lakes and rivers with fluctuating water levels and river flows, fishing effort has been found to vary between years (Tilzey 1978, North 1980). Since this study was during a period of low lake levels due to drought conditions it is likely that,

over the longer term and in years of higher lake level, fishing effort would be higher than the estimate derived.

A further underestimate of the long-term (and present) total fishing effort arises from the omission of the darkness fishing effort, estimated from interviews to be about 27% of the daylight effort. The reliability of this estimate is questionable since anglers who commenced fishing after dark and finished before dawn were not interviewed. In general, other surveys have not included night fishing estimates unless they were based on postal interviews. Further studies would be required to determine the effects of higher lake level, inflow and night fishing on fishing effort.

Recreational anglers catch the majority of fish taken from Australian inland waters (Tilzey 1978). The estimated total yield of edible fish from Lake Keepit in the 1981/82 season (52 tonnes) was equivalent to 14% of the total recorded NSW commercial catch of freshwater fish in 1980/81 (372 tonnes).

The mean weight of an individual fish (1.2kg) from Lake Keepit is exceptionally high when compared with most other studies except Lake Eucumbene (1kg) (Tilzey 1978). For example, the average weight of retained fish in Botany Bay (SPCC 1981) and Lake Macquarie (Henry and Virgona 1980) was 0.4kg and 0.2kg, while the annual catch rates were 55 and 35 fish/ha, respectively. At Lake Keepit it was 27 fish/ha. These data emphasise the point that while relatively fewer fish are caught at Lake Keepit they are of a larger size than at other places studied, except Lake Eucumbene, and this contributes to the high angling catch figure (32 kg/ha) for Lake Keepit. Furthermore, the population structure of Golden Perch indicates that most of the fish angled belonged to the one, IV-V age class (unpublished data). The dependence on one age class suggests that the mean size and number of fish caught would alter in future years depending on the time between successful spawnings, recruitment and growth rates.

A greater percentage of anglers belonged to fishing clubs (30%) than has been found in other surveys in Australia, e.g. 5% in Sydney Harbour (Henry 1984). The high incidence of fishing club membership at Lake Keepit could be useful for further fisheries management of the lake since information on fishing effort, catch and CPUE could be supplied by local fishing clubs on a regular basis.

This creel survey's primary objective was to estimate annual catch and effort by monthly sampling. According to Malvestuto *et al.* (1979), maximum accuracy of annual estimates is attained when allocation of sampling effort is proportional to monthly variation in catch or effort by anglers. During the planning stages of this creel survey, this variation was unknown and the best approach available was to allocate sampling equally between months. Optimum allocation of sampling effort in future surveys would now be possible although another 12 months data would be preferable to fine tune this allocation.

LAKE KEEPIT CREEL SURVEY

In conclusion, this creel survey has shown that Lake Keepit supports an excellent recreational fishery comparable to coastal Australian and overseas fresh-water fisheries. The lake is especially important to locally-based anglers. While fishing efforts are of the same order of magnitude as other recreational fisheries, the yield of fish (kg/ha) is greater than has been previously reported for a warm-water fishery. It is also likely that long-term fishing effort has been underestimated due to the study being conducted in a drought year and there being no accurate estimate of night fishing. The high degree of variability associated with monthly fishing efforts and CPUE estimates, and the lack of comparative data indicates the need for more extensive longer term investigation of this and other such fisheries throughout the State.

ACKNOWLEDGEMENTS

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Two New *Argulus* Species (Branchiura: Argulidae) Found on Australian Bream (*Acanthopagrus* spp.)

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ABSTRACT

Two species are described: *Argulus australiensis*, new species from *Acanthopagrus berda* (Forskal), and *Argulus diversicolor*, new species from *Acanthopagrus latus*. (Houttuyn).

INTRODUCTION

From May, 1982 to January, 1983, I collected and examined approximately 1,000 *Acanthopagrus* specimens, i.e. *A. berda*, *A. latus*, *A. butcheri* and *A. australis* from around Australia in order to assess the ectoparasite fauna of the economically important bream.

Argulus species found in this study are the first records from Australian marine waters. *Argulus macropterus* Heegaard (1962) on a *Mugil* sp. from the Murray River and the cosmopolitan *A. japonicus* Thiele (1900) from *Carassius auratus* at a Sydney freshwater aquarium are the only other members of this genus recorded in Australia.

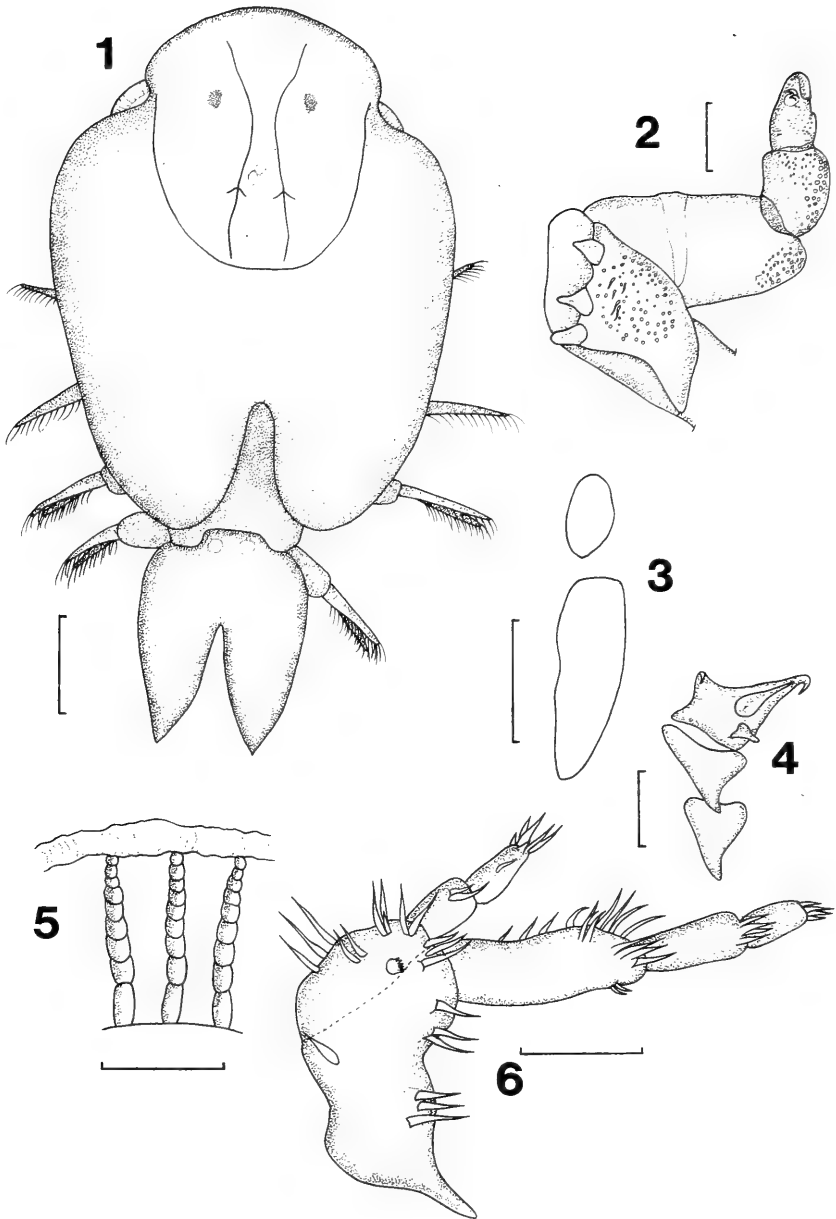
MATERIAL AND METHODS

Samples of at least 40 fish per species, per site were collected at 23 localities from around Australia (all states).

Immediately after capture, fish were killed by pithing, their ventral body wall slit open, and they were dropped into 10% formalin. The body surface, fins, head, nares, mucous cavities, pseudobranchs, individual gill filaments and gill arches of each fish were examined under a dissecting microscope. The sediment resulting from dissection and that left in the drum containing the preserved fish were also examined.

Specimens were taken from 10% formalin and washed in distilled water before being stored in 70% ethanol. All parasites were cleared, dissected and examined in lactic acid. Standard cavity slides were used to hold specimens being measured in order to reduce compression by the coverslip.

Parasites were measured with a calibrated ocular micrometer. Measurements are given in micrometers. All drawings were made with the aid of a camera lucida.



Argulus australiensis, sp. nov.

Fig. 1. Female, dorsal. Fig. 2. Maxilliped, ventral. Fig. 3. Respiratory areas, ventral.

Fig. 4. First antenna, ventral. Fig. 5. Ribs of sucker. Fig. 6. Second antenna, ventral.

Scale lines: (1) 980 μm . (2) and (4) 250 μm . (3) 1,000 μm . (5) and (6) 100 μm .

NEW AUSTRALIAN ARGULIDS

SUBCLASS Branchiura

ORDER Argulidea

FAMILY Argulidae Leach

GENUS *Argulus* Müller

Argulus australiensis, sp. nov.

MATERIAL

One male and one female specimen collected. Female holotype and male allotype, deposited in Australian Museum (P35479 and P35480).

SITE

Unknown, specimens were found in debris of fish sample.

HOST

A. berda.

LOCALITY

Karumba, Queensland.

DESCRIPTION

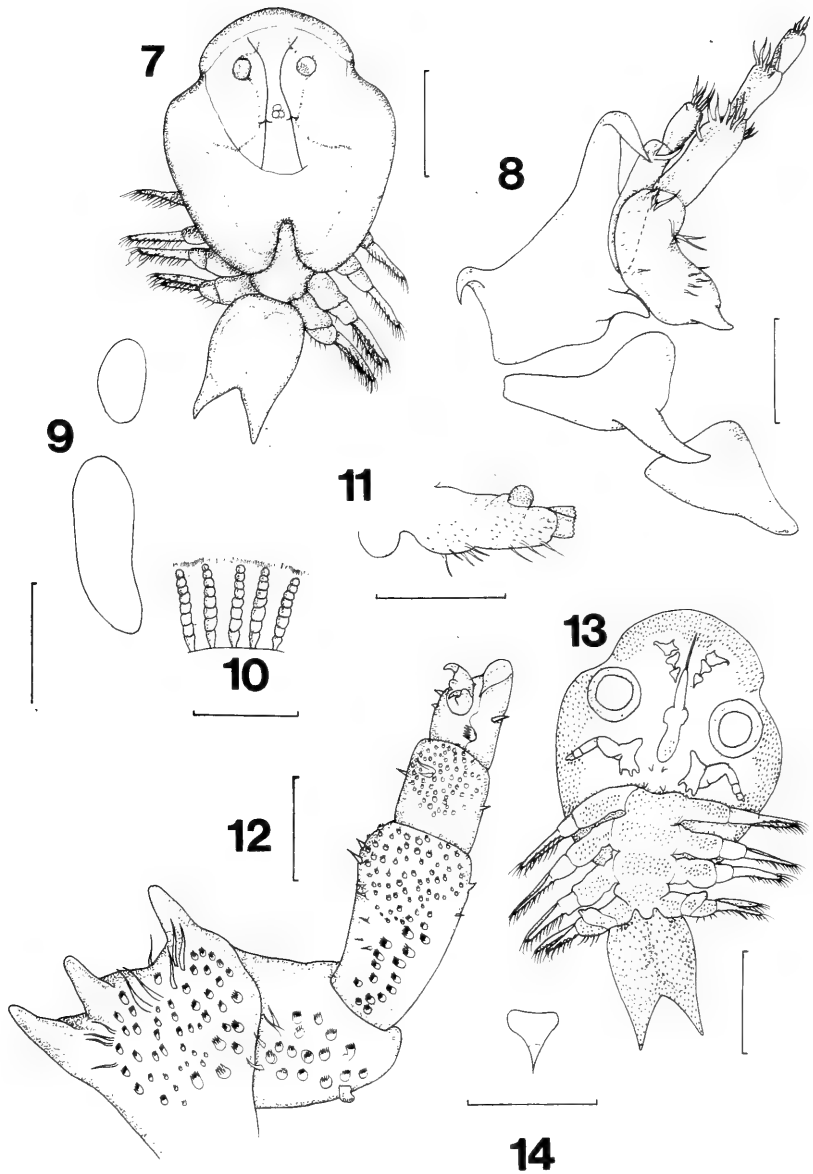
Female (Figs 1-6).

Measurements based on one specimen. Preserved specimen greenish-yellow in colour. Total length 7,350. Carapace elliptical, 5,150 x 4,018 (Fig. 1). Transverse groove arched upwards. Dorsal submedian ridges converge most closely between the large eyes then gradually diverge towards anterior and posterior ends. Lateral lobes rounded, posterior corners extending to bases of fourth pair of legs. Median posterior sinus deep, leaving portion of free thoracic region exposed.

Abdomen bilobed, longer than broad, 2,200 x 1,670, more than one quarter total length. Anal laminae small, barely projecting through bases of anal slits.

Respiratory areas (Fig. 3) of unequal size, much smaller anterior area. First antenna (Fig. 4) with stout basal spine which covers portion of postantennal spine; lateral hook reinforced by curved accessory spine; flagellum (Fig. 4) two-segmented and setose. Second antenna (Fig. 6) four-segmented; proximal segment armed posteriorly with a strong spine and a number of setae, distal segment with four apical setae.

Suckers large, 1,120 in diameter, ribs consisting of nine disks (Fig. 5). Maxilliped (Fig. 2) five-segmented; basal segment with three large, flat spines, one terminal and two subterminal spines. Chitinous plates on maxilliped with comb-like projections.



Argulus australiensis, sp. nov.

Fig. 7. Male, dorsal. Fig. 8. First and second antennae, ventral. Fig. 9. Respiratory areas, ventral. Fig. 10. Ribs of sucker. Fig. 11. Basal portion of fourth leg, ventral. Fig. 12. Maxilliped, ventral. Fig. 13. Male, ventral. Fig. 14. Tooth-like process.

Scales lines: (7) and (13) 1,000 μm . (8), (10) and (12) 100 μm . (9) and (11) 500 μm . (14) 50 μm .

NEW AUSTRALIAN ARGULIDS

Swimming legs biramous, all project beyond lateral margins of carapace. Fourth leg with small lobe and a number of setae on posterior margin of basal segment.

Anterior and lateral margins of carapace, basal segments of swimming legs and abdomen covered ventrally with small, tooth-like spines.

Mouth tube about twice as long as wide and with ornamentation at base.

Male (Figs 7-14).

Measurements based on one specimen. Preserved specimen pale yellow with two distinct bands of brown pigment (Fig. 7). Total length 4,160. Carapace 2,530 x 2,140, similar in shape to that of female although not reaching as far posteriorly.

Abdomen 1,330 x 820 bilobed but lobes not separated as much as in female. Spermatheca (Fig. 7) about three-quarter length of abdomen.

Respiratory areas (Fig. 9) similar to that of female. First antenna (Fig. 8) without accessory spine. Second antenna (Fig. 8) similar to that of female.

Suckers large (Fig. 13) 550 in diameter, ribs consisting of eight disks (Fig. 10). Maxilliped (Fig. 12) as in female except for an increased number of setules.

Swimming legs biramous, extending further from margins of carapace than in female. Basal portion of fourth leg modified as shown (Fig. 11).

Portions of ventral surface covered by tooth-like spines (Figs 13, 14).

ETYMOLOGY

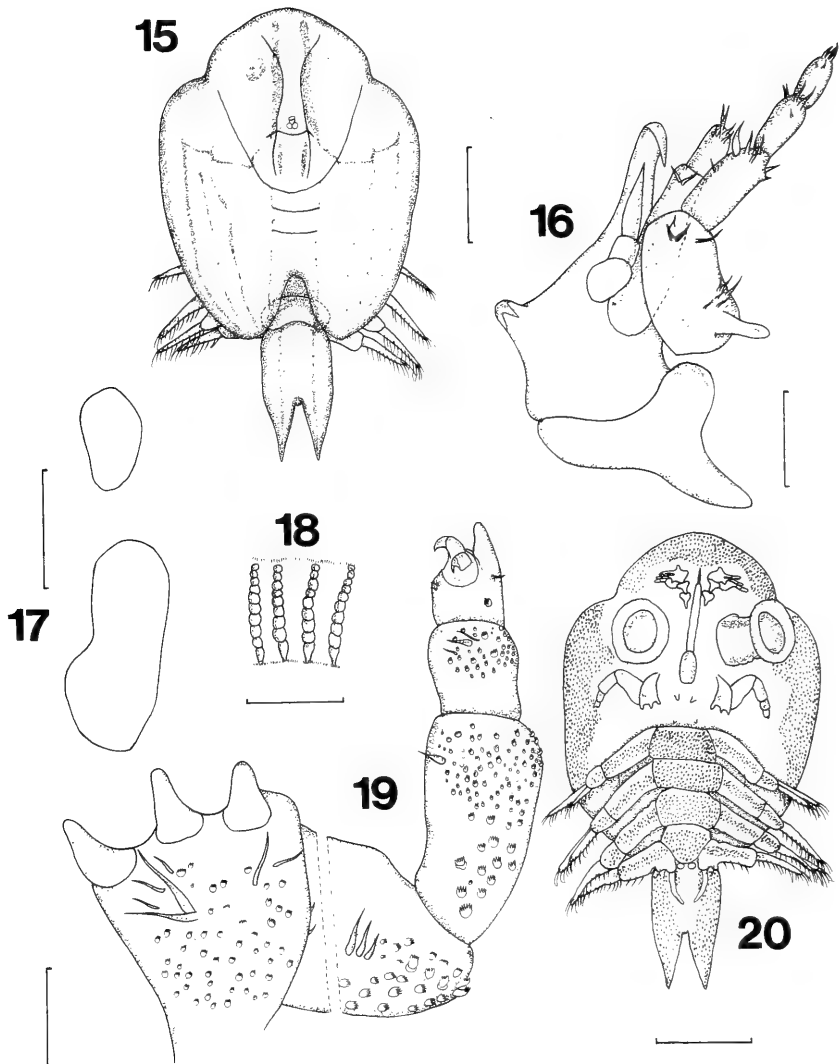
The name *australiensis* refers to the fact that this is the first marine argulid to be described from Australian waters.

DISCUSSION

The present species is most similar to *Argulus diversicolor* described below. However, the new species lacks distinctive streaks on its dorsal surface, is larger, has a more rounded and robust abdomen, and has only nine disks in its sucker ribs compared with ten in *A. diversicolor*. The male is most similar in general character to *A. alexandrensis* Wilson (1923) from *Zeus* sp. in South Africa but can be easily distinguished from it by the shape of its carapace which is not as evenly elliptical and by its transverse groove which does not extend as far anteriorly as in *A. alexandrensis*.

DIFFERENTIAL DIAGNOSIS

The female is distinguished by the shape of the carapace and respiratory areas as well as the armature of the antennae.



Argulus diversicolor, sp. nov.

Fig. 15. Female, dorsal. Fig. 16. First and second antennae, ventral. Fig. 17. Respiratory areas, ventral. Fig. 18. Ribs of sucker. Fig. 19. Maxilliped, ventral. Fig. 20. Female, ventral.

Scale lines: (15) and (20) 1,000 μ m. (16) (18) and (19) 100 μ m. (17) 500 μ m.

NEW AUSTRALIAN ARGULIDS

The male differs from other species in the combination of the shape of the carapace, armature of the antennae and the number of the dorsal ribs.

Argulus diversicolor, sp. nov.

MATERIAL

One female collected. Female holotype from *A. latus* at Point Samson, deposited in Australian Museum (P35481).

SITE

Gill filaments.

HOST

A. latus

LOCALITY

Carnarvon, Western Australia.

DESCRIPTION

Female (Figs 15-20).

Measurements based on one specimen. Preserved specimen smokey brown with a series of longitudinal deep brown bands running along carapace and abdomen (Fig. 15). Total length 4,800. Carapace elliptical, 3,510 x 2,740. Transverse groove arched upwards. Dorsal submedian ridges closest together between the large eyes, gradually diverging anteriorly and posteriorly. Lateral lobes rounded; posterior corners extending to, and nearly covering bases of fourth pair of legs. Median posterior sinus extending to base of second pair of swimming legs, with portion of free thoracic region exposed.

Abdomen bilobed, longer than wide, 1,410 x 780, more than one quarter total length. Anal laminae small, just visible projecting through bases of anal slits.

Respiratory areas (Fig. 17) of unequal size, much smaller anterior area. First antenna (Fig. 16) with stout basal spine which covers basal portion of postantennal spine; lateral hook bearing an accessory spine; flagellum two-segmented and setose. Second antenna (Fig. 16) four-segmented; proximal segment armed posteriorly with a strong spine and ten setae; distal segment with five setae (three terminal and two subterminal).

Suckers large (Fig. 20) 650 in diameter; ribs consisting of nine to ten disks, basal element longest (Fig. 18). Maxilliped (Fig. 19) five-segmented; basal segment with three large spines; terminal segment with an outer blade-like spine

and two inner sharply curved spines as well as a single comb-like process; all segments armed with setules and comb-like processes.

Swimming legs biramous, all project beyond lateral margins of carapace. Anterior and lateral margins of carapace, basal segments of swimming legs and abdomen covered ventrally with many tooth-like spines (Fig. 20). Mouth tube larger than wide, ornamentation at base.

No male found.

ETYMOLOGY

The name *diversicolor* refers to the characteristic longitudinal bands of pigment on the dorsal surface.

DISCUSSION

The present species is most similar to *A. matuii* Sikama (1938) collected in Japanese waters from *Parapristipoma trilineatum* (Thunberg). Both species have characteristic highly pigmented streaks or bands on their dorsal surfaces. However, *A. diversicolor* is most readily separated from *A. matuii* by the following characters: the presence of an accessory spine on the lateral hook of the first antenna, *A. matuii* has none; the number of crescentic disks of the suckers, *A. diversicolor* has nine to ten, *A. matuii* has fourteen to fifteen; more elongate shape of the respiratory area of the new species, and size of body proper, *A. diversicolor* is only about half the length of *A. matuii*.

DIFFERENTIAL DIAGNOSIS

The female differs from other species in the combination of the following: pigment bands on the dorsal surface, armature of the first antenna and the number of disks on the sucker ribs.

ACKNOWLEDGEMENTS

This paper represents part of a Ph.D. thesis completed in the Zoology Department, University of New England. Advice and criticism was provided by Dr R. Cressey and Dr K. Rohde. A portion of this study has been supported with an International Institute of Education Fellowship and a University of New England Scholarship. Mrs V. Watt typed the final manuscript. To all the above, and to the many people who assisted in the field, I extend my deepest gratitude.

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Records of Parasitism by Members of the Family Tachinidae (Diptera: Tachinidae)

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ABSTRACT

About 84 species of Tachinidae are recorded from approximately 61 hosts. The latter belong to the following orders: Mantodea 1, Orthoptera 1, Hemiptera 1, Coleoptera 8, Lepidoptera 47, and Hymenoptera 3. Data are given on the relationship of tachinid and host, distribution and monthly occurrence of the flies.

INTRODUCTION

Over a period of many years tachinid adults have been bred from insects under investigation in the laboratories of the N.S.W. Department of Agriculture and added to the insect collection, for which the authors were formerly responsible. Many of the hosts, especially in the Order Lepidoptera, are pest species, consequently the data may be of interest in applied entomology.

Initials are used for the following collectors: T. V. Bourke, C. E. Chadwick, W. W. Froggatt, G. J. Goodyer, L. R. Greenup, J. T. Hamilton, M. S. Moulds, H. E. Osburne, V. J. Robinson and W. E. Wright. Other collectors are named in full.

When R. W. Crosskey was revising the Australian Tachinidae, numerous specimens were sent to him at the British Museum (Natural History) for determination. Since then some identifications have been made by K. M. Harris and B. Cantrell; these are indicated by bracketed initials.

Genera are arranged alphabetically in the parasite-host list and the order and family of the host mentioned only in the first recording. The nomenclature is that of Crosskey (1973).

ABBREVIATIONS

Insect orders are abbreviated as follows:

C. = Coleoptera

He. = Hemiptera

Hy. = Hymenoptera

L. = Lepidoptera

M. = Mantodea

O. = Orthoptera

The abbreviation n.d. means no date given.

PARASITIC GENERA OF THE FAMILY TACHINIDAE RECORDED HEREIN

Subfamily PHASIINAE

Phasiini: *Alophora*. Leucostomatini: *Leucostoma*.

Subfamily PROSENINAE

Prosenini: *Senostoma*.

Subfamily TACHININAE

Palpostomatini: *Palpostoma*. Campylochetini: *Elpe*. Voriini: *Voria*. Leskiini: *Apatempia*. Linnaemyini: *Chaetophthalmus*. Tachinini: *Microtropesa*.

Subfamily GONIINAE

Acemyini: *Ceracia*. Neaerini: *Voriella*. Siphonini: *Actia*, *Ceromyia*, *Peribaea*. Blondeliini: *Anagonia*, *Compsilura*, *Medinodexia*, *Monoleptophaga*, genus near *Pareupogona*, *Trigonospila*. Exoristini: *Austrophorocera*, *Eozenillia*, *Exorista*, *Stomatomyia*. Winthemiini: *Winthemia*. Carceliini: *Carcelia*, *Carcelimyia*. Anacamptomyiini: *Anacamptomyia*. Sturmiini: *Anamastax*, *Blepharipa*, *Palexorista*, *Paradrino*, *Sisyropa*, *Sturmia*, *Tritaxys*, *Zygobothria*. Goniini: *Coniophthalmus*. Eryciini: *Alomyia*, ?*Austrophyno*, *Chlorogastropsis*, *Teretrophora*.

PARASITE-HOST RELATIONSHIPS

Actia eucosmae Bezzi. Ex larva *Crociosema plebeiana* Zell., (L., Tortricidae), Wee Waa, 20/1/63, D. Taylor.

Alophora lepidofera (Mall.). Ex adults *Nysius vinitor* Berg., (He., Lygaeidae), Leeton, 1/11/71.

Anacamptomyia nigriventris (Mall.). Ex *Polistes tasmaniensis* Sauss., (Hy., Vespidae), Ryde, 18/4/50; ex nest *Polistes* sp., Canyon Camp, Warrumbungle Nat. Pk., 15, 22/5/67. C.E.C.

Anagonia sp. nr. *lateralis* (Macq.). Ex adult *Bryachis squamicollis* Pasc., (C., Curculionidae), Dubbo, 24/1/09.

Anagonia sp. Depositing egg on paropsine larva, (C., Chrysomelidae), Mt. Wilson, 14/2/60, C.E.C.

Anamastax sp. nov. Ex larvae *Panacela lewinae* (Lew.), (L., Eupterotidae), Bilpin, 29/11/71, 10/12/71, P. Smart (collected on *Eucalyptus* sp.)

- Apatemyia* ?sp. nov., nr. *longiceps* Macp. Ex larva *Phloeoglymma dorsalis* (Pasc.), (C., Curculionidae), Brooklyn, 10/8/69, 22/10/69, 2/12/69, C.E.C. Host larva boring in stem *Astrotricha floccosa* coll. 13/7/69.
- Apomyia* sp. Ex larva *Zizina otis labradus* (Godt.), (L., Lycanidae), Camden, 1/3/72, G.J.G. (K.M.H.).
- Austrophorocera grandis* (Macq.). Ex cocoon *Doratifera vulnerans* (Lew.), (L., Limacodidae), Meadowie, 18/10/01, Miss Cole (B.C.); ex *D. vulnerans*, Northwood, 20/12/27, A. R. Woodhill; ex *D. vulnerans*, Port Stephens, 24/10/38, (B.C.); ex cocoon *D. ?quadriguttata* Walk., Rydalmere, 29/6/65, C.E.C.
- A. sp. nr. grandis*. Ex cocoon *D. casta* Scott, Wagga, 18/1/60, J. R. Sutherland.
- A. sp. 1*. Ex *Doratifera* sp., Moore, 1918, W.W.F.
- A. sp. 2*. Ex anthelid larva, Roseville, 14/3/72, C.E.C. (K.M.H.).
- ?*Austrophyrno* sp. Ex *Perga* sp., (Hy., Pergidae), Upper Kangaroo Valley 25/3/51, C.E.C.
- Blepharipa fulviventris* (Macq.). Ex pupa *Papilio aegeus aegeus* Don., (L., Papilionidae), Cronulla, 3/4/57; do., Collaroy, 2/1/62, M. J. Gaven; ex *Theretra nesus* (Drury), (L., Sphingidae), Bellingen, 8/7/66, V.J.R.
- B. sp. nr. fulviventris* (Macq.). Ex cocoon *Anthela acuta* Walk., (L., Anthelidae), North Ryde, 19/3/75, C.E.C.
- B. sp. sugens* group. Ex pupa *Graphium sarpedon choredon* (Feld.), (L., Papilionidae), Greenwich, n.d., M.S.M. (K.M.H.).
- B. sp. 1*. Ex larva *Teia anartoides* Walk., (L., Lymantriidae), Rydalmere, 15/12/64.
- B. sp. 2*. Ex pupa *Papilio aegeus aegeus*, Newport Beach, 22/3/64, B. Welch.
- Carcelia illota* (Curran). Ex larva *Heliothis* sp., (L., Noctuidae), Coffs Harbour, 2/1/40.
- C. murina* (Curran). Ex *Anthela* sp., Uralla, 30/9/15, W.W.F.; ex pupa *Anthela varia* Walk., 5 km. North of Barrington, 8/12/68. V.J.R.: ex pupa *Anthela* sp., Paroo River, 10/3/74, V.J.R.
- **C. sp. 1*. Ex cocoon ?*Anthela acuta*, Wollongong, 17/10/50, C.E.C. *(*acteosa*).
- **C. sp. 2*. Ex *Delias aganippe* Don., (L., Pieridae), Glen Innes, 17/3/68 M.S.M. *(*kindaichin*).
- **C. sp. 3*. Ex cocoon *Teia anartoides*, Sydney, -/3/09.
- Carcelimyia dispar* (Macq.). Ex *Panacela lewinae*, Cataract Dam, 15/12/64, V.J.R.

* To be named in forthcoming paper by B. Cantrell.

- Ceracia fergusonii* (Mall.). Ex *Chortoicetes terminifera* (Walk.), (O., Acrididae), Condobolin, 19/6/28, J.T.G. Avel; do., Curban, nr. Gilgandra, 23/2/70, (lab. bred), M. Casimir; do., Wilbur Downs, nr. Coonamble, 10/2/71, (lab. bred), C. Gauchat; do., do., 25/5/71, 29/6/71, (lab. bred), C. Gauchat.
- Ceromya norma* (Mall.). Ex *Mythimna convecta* (Walk.), (L., Noctuidae), (parasite pupated externally), Griffith, 24/3/67, D. Wallin; do., Rydalmere, 28/9/67, L.R.G.; do., Kangaroo Valley, 15/11/67, L.R.G.
- C. parviseta* (Mall.). Ex *Isotenes miserana* (Walk.), (L. Tortricidae), Kurnell, 17/10/70, V.J.R.
- Chaetophthalmus bicolor* (Macq.). Ex jar of soil in which larvae of *Agrotis infusa* (Boisd.) had been bred out, Red Range, nr. Glen Innes, late Dec. 1950, (B.C.); ex *Sericesthis geminata* Boisd., (C., Scarabaeidae), 11/10/57, T.V.B. (B.C.) DOUBTFUL; ex late instar *Agrotis munda* Walk., (L., Noctuidae), Rydalmere, 16/12/71.; ex larva *Agrotis munda*, Rydalmere, early December 1971, G.J.G., (B.C.).
- C. biseriatus* Mall. Ex pupa *Persectania ewingii* (Westw.), Sutton Forest, 1/1/65, K. Giles, (B.C.); ex larva *Heliothis* sp., Narrabri, 11/10/68, J.T.H.; ex larva *Heliothis* sp., 13/10/71, G.J.G., (B.C.); ex larva *Heliothis punctigera*, Cowra, 26/11/71, G.J.G., (B.C.); ex late instar larva *Heliothis* sp., Narrabri, -/3/73, J.T.H.
- C. sp.* Ex *Mythimna convecta*, Berry, 5/1/67, L.R.G., (parasite pupated externally).
- C. sp.* Ex larva *Heliothis* sp., Bathurst, 18/1/67, L.R.G. (parasite pupated externally).
- Chlorogastropsis orga* (Walk.). Ex *Oiketicus elongatus* Saund., (L. Psychidae), N.S.W. 18/10/16; do., Sydney -/2/28, W. B. Gurney; do., Heathcote, 7/2/50, C.E.C.; do., Greenacre, -/8/58, T.V.B.; do. (larva), Merrylands, 28/7/60; do., West Ryde, 2/10/63, L. F. Pratt; do., Wollongong, 18/1/65, V.J.R.; do., Helensburgh, -/10/68, H.E.O.
- Chlorogastropsis* sp. nov. Ex *Araeostoma aenicta* Turn., (L., Xyloryctidae), Windang, 15/9/66, V.J.R.
- Compsilura concinnata* (Meig.). Ex *Isotenes miserana* (= *Cacoecia australana*), Northwood, -/1/29, A. R. Woodhill; ex *Doratifera vulnerans*, Manly, 10/9/41; ex pupa *Artogeia rapae* (L.), (L., Pieridae), Windsor, -/5/72, J.T.H.; ex armyworm (L., Noctuidae), Murwillumbah, 30/5/55, B. M. Braithwaite.
- Elpe* sp. Ex *Panacela lewinae*, Cowra Dist., 1904.
- Eozenillia remota* (Walk.). Ex *Hylarcta huebneri* (Westw.), (L., Psychidae), Maroubra, -/9/23, E. H. Zeck; do., Armidale, 3/3/34; ex case *H. nigrescens* (Doubld.), Cowra, 17, 24/4/52; do., Gosford, 17/7/67, P. C. Hely; ex *Anthela ariprepes* Turn., (L., Anthelidae), 5 km N. of Barrington, (n.d.), V.J.R.

PARASITISM BY THE FAMILY TACHINIDAE

- Exorista coras* (Walk.). Ex *Pseudomantis albofimbriata* Stal, (M., Mantidae), Roseville, 19/11/58, C.E.C.
- E. curriei* (Curran). Ex larva *Heliothis punctigera*, Cowra, 26/11/71, G.J.G. (B.C.).
- E. flaviceps* Macq. Ex larva *Uraba lugens* Walk., (L., Nolidae), Tamworth, 19/11/53, L. F. Pratt.
- E. psychidivora* (Coq.). Ex pupa *Phalaenoides glycine* Lew., (L., Agaristidae), Richmond, -/12/02, 15/1/03, 20/1/03, W. B. Gurney; ex *Hyalarcta nigrescens* (= "*Thyridopteryx herrichi*"), Yanco, -/6/16; ex larva *Teara contraria*, Broken Hill, 5/7/68; (All B.C.).
- E. sorbillans* (Wied.). Ex *Spodoptera exempta* (Walk.), (L., Noctuidae), Wagga, 5/7/63.
- Goniophthalmus australis* (Bar.). Ex pupa *Spodoptera exempta*, Uki, 8/3/66, L.R.G.; do., Warrell Ck., 19/4/66, L.R.G.
- G. rufescens* (Bar.). Ex *Neocleptia punctifera* Walk., (L. Noctuidae), Warren, 16, 30/6/39.
- Leucostoma simplex* (Fallen). Ex adults *Nysius vinitor*, Leeton, 1/11/71.
- Medinodexia morgani* (Hardy). Ex adult *Aulacophora hilaris* (Boisd.), (C., Chrysomelidae), Biniguy, 22/2/30, W. L. Morgan, (lectotype and paralectotype); do., Narara, 11/11/31, 21/11/31, W. L. Morgan.
- Microtropesa flaviventris* Mall. Ex larva *Mythimna convecta* (= "*Cirphis unipuncta* Haw."), Newbridge, -/1/35, N. S. Noble; ex pupa *Persectania ewingii*, Albury, 25/11/65, R. J. Flynn; ex larva *P. ewingii*, Sutton Forest, 15/12/65, G. Giles; ex *Mythimna convecta*, Taree, 25/4/66, L.R.G.; ex larva *Persectania ewingii*, Sydney, 20/10/67, F. McDonald.
- Monoleptophaga caldwelli* Bar. Ex *Monolepta australis* (Jac.), (C., Chrysomelidae), Lismore, 16/10/92, D. McDonald.
- Palexorista macquarti* (Cross.). Ex *Doratifera* sp., Yenda, 4/4/51, Stanton (host from leaves *Eucalyptus crebra*).
- P. sp. nr. macquarti* (Cross.). Ex pupa *Diggleisia australasiae* (F.), (L., Lasiocampidae), Beecroft, 18/2/72, C.E.C.
- P. sp. nr. macquarti* (Cross.). Ex larva Sphingidae, Sydney 2/7/59; ex pupa *Diggleisia australasiae*, Beecroft, 18, 19-20/2/72, C.E.C.
- P. spp.* Ex sphingid on grape vine, Trundle, 2/5/28; ex noctuid larva, Hartley Vale, 23/1/28; ex *Spodoptera exempta*, Grafton, 7/4/36; ex case moth, Yass, 3/11/54; ex *Persectania* sp., Albury, 25/11/65, R. J. Flynn; do., Sydney University, 20/11/66, L.R.G.; ex *Archernis mitis* Turn., (L., Pyralidae),

- Grafton, 15, 16/2/67; *Mythimna convecta*, Oakville, 13, 14, 15, 16/3/67, L.R.G.
- Palpostoma* prob. *subsessile* Mall. Ex adult *Metanastes blackburni* Arrow, (C., Scarabaeidae), Kempsey, 20/9/40; ex adult *Heteronychus arator* (F), (C., Scarabaeidae), Kempsey, 20/9/40.
- P. testaceum* R.-D. Ex adult *Heteronychus arator*, Maclean, 17/9/53, W.E.W.
- Palpostoma* sp. ex adult *Metanastes blackburni*, Woy Woy, 25/12/31, R. W. Burrell; do Kempsey, 20/9/40; ex dead adult *Heteronychus arator*, Kangaroo Valley, 26/8/53, W.E.W.
- Paradrino laevicula* Mesnil. Ex *Delias aganippe* Don., (L., Pieridae), Glen Innes, 4/3/67, M.S.M.
- Gen. nr. *Pareupugona*. Ex *Anthela acuta*, Wollongong, 18/4/63, V.J.R.
- Peribaea argentifrons* (Mall.). Ex *Copromorpha prasinichroa* Meyr., (L., Copromorphidae), Minnamurra Falls, 1/7/69, V.J.R.
- P. plebeia* (Mall.). Ex larva ?*Anthela* sp., Roseville, 27-29/11/71, C.E.C.
- Senostoma* sp. Ex adult *Sericesthes geminata* Boisdl., (C., Scarabaeidae), Dorrigo, 24/9/57, T.V.B.
- Sisyropa* sp. Ex either pupa or larva *Hymenia recurvalis* (F.), (L., Pyralidae), Graman, 20/5/59, T.V.B.
- Stomatomyia tricholygoides* Bezzi. Ex *Mythimna convecta* (= "*Cirphis unipuncta* Haw."), Gerringong, 25/2/47, J. A. Wright; ex larva *Loxostege affinitalis* (Led.), (L., Pyralidae), Garah, 7/4/34; ex *Amata* sp. ?*xanthura* Turn., (L., Amatidae), Werris Ck., 2/10/53; ex *Spodoptera exempta*, Warrell Ck., 19/4/66, L.R.G.; ex *Mythimna convecta*, Taree, 20/4/66, L.R.G.
- Sturmia convergens* (Wied.). Ex pupa *Danaus plexippus plexippus* (L.), (L., Nymphalidae), Cobbitty, 27, 30/5/62, E. B. Skreen.
- Teretrophora fasciata* Macq. Ex *Garrha hemiteles* (Meyr., (L. Oecophoridae), Mt. Keira, 10/10/70, V.J.R.; ex *Philobota fascialis* F., (L., Oecophoridae), Mt. Keira, 24/9/70, V.J.R.
- Trigonospila brevifascies* Hardy. Ex *Garrha hemiteles*, Carrington Falls, 9/10/70, V.J.R.
- Tritaxys heterocera* (Macq.). Ex (probably) larva *Plutorectis caespitosae* Oke, (L., Psychidae), Mt. Kosciusko, 8/6/47, A. Williams.
- T. scutellata* (Macq.) Ex *Mythimna convecta* ("*Leucania* = *Cirphis unipuncta* Haw."), 1903; do., ("*Cirphis unipunctata*"), Bellingen, 7/3/31; do., Newbridge, -/1/35; do., Albion Park, -/3/36; ex larva *Agrotis* sp., (L., Noctuidae),

- Wyong, 25/9/40; ex *Mythimna convecta*, Windsor, 30/10/47, C.E.C.; do., (emerged from jar containing larvae and pupae), Shellharbour, -/4/49, C. R. Wallace; ex *Mythimna convecta*, Inverell, 10/12/66, L.R.G., (parasite pupated externally); do., Kangaroo Valley, 29, 30/12/66, 2/11/67, L.R.G. (parasite pupated externally); do., Berry, 16/1/67, L.R.G., (parasite pupated externally); do., Ourimbah, 21/4/67, L.R.G., (parasite pupated externally); do., (ex pupa), Nowra, 10/12/67, L.R.G., (parasite pupated externally).
- T. milias* (Walk.). Ex larva of Noctuidae, Sydney, 6/1/27; ex jar of soil in which larvae of *Agrotis infusa* were bred out, Red Range, nr. Glen Innes, early January 1951; ex larva *Persectania ewingii*, Berrigan, 14/12/53, G. R. Godden; ex *Agrotis infusa*, Parkes, 5/10/65, L.R.G.; do., Dalgety, 23/11/70, I. Collett.
- T. sp.* ?nov. Ex pupa *Persectania ewingii*, Albury, 19/12/65, R. J. Flynn.
- Voria ruralis* (Fallen). Ex *Chrysodeixis* (= *Phytometra*) *argentea* Guen., (L., Noctuidae), Royal Botanic Gardens, Sydney, 1-17/12/48, R. New; do., Texas, Qld., -/1/49, W. L. Morgan; do., (ex larva), Erina Hts., 29/10/63, J. G. Gellatley; do., (ex pupa), Narrabri A.R.S., 4/2/69, W.E.W.
- Voriella uniseta* Mall. Ex lucerne infested with *Merophyas* (= *Tortrix*) *divulsana* (Walk.), (L., Tortricidae), Richmond, 14/12/54, R. D. Power; ex *Epiphyas postvittana* (Walk.), (L., Tortricidae), Bathurst, 11/4/56, N. C. Lloyd; ex larva *Cydia molesta* (Busck), (L., Tortricidae), Castlereagh, 16/2/61, M. J. Gaven.
- Voriella sp.* Ex *Epiphyas postvittana*, Bundanoon, 28/1/71, V.J.R.
- Winthemia lateralis* (Macq.). Ex larva *Agrotis* ("Euxoa") sp., Wyong, 25/9/40, (B.C.); ex *Mythimna convecta* (= "*Cirphis unipuncta* Haw."), Wyong, 25/9/40, (B.C.).
- W. neowinthemoides* (Townsend). Ex pupa *Euploea core* (Cram.), (L., Nymphalidae), Newcastle, 29/3/50; ex *Danaus plexippus plexippus*, Sydney, -/4/53; ex pupa *Euploea core*, Kempsey, 8/6/53, F. C. McLeary; ex larva *Leptocneria reducta* (Walk.), (L., Lymantriidae), Penrith, 16/5/60, M. J. Gaven; ex pupa *Danaus plexippus plexippus*, Cobbitty, 30/5/62, E. B. Skreen; ex *Delias aganippe*, Glen Innes, 3/3/67, M.S.M.; ex *Danaus plexippus plexippus* Wollongong, -/4/67; ex *Mythimna convecta*, Nowra, 10/12/67; ex *Danaus plexippus plexippus*, Greenwich, 1971, M.S.M. (All B.C.).
- Zygobothria atropivora* (R.-D.). Ex *Psilogramma menephron* (Cramer) (= "*Macrosila casuarina*",) Sydney, n.d.

HOST-PARASITE RELATIONSHIPS

MANTODEA

MANTIDAE

Pseudomantis albofimbriata: *Exorista coras*.

ORTHOPTERA

ACRIDIDAE

Chortoicetes terminifera: *Ceracia fergusoni*

HEMIPTERA

LYGAEIDAE

Nysius vinitor: *Alophora lepidofera*, *Leucostoma simplex*.

COLEOPTERA

SCARABAEIDAE

Sericesthis geminata: *Chaetophthalmus bicolor*, *Senostoma* sp.

Heteronychus arator: *Palpostoma* prob. *subsessile*, *P. testaceum*.

Metanastes blackburni: *Palpostoma* prob. *subsessile*, *Palpostoma* sp.

CHRYSOMELIDAE

Aulacophora hilaris: *Medinodexia morgani*.

Monolepta australis: *Monoleptophaga caldwelli*.

Paropsinae: *Anagonia* sp.

CURCULIONIDAE

Bryachus squamicollis: *Anagonia* sp. nr. *lateralis*.

Phloeoglymma dorsalis: *Apatemyia* ?sp. nov. nr. *longipes*.

LEPIDOPTERA

TORTRICIDAE

Crociosema plebeiana: *Actia eucosmae*.

Cydia molesta: *Voriella uniseta*.

Epiphyas postvittana: *Voriella uniseta*, *Voriella* sp.

Isotenes miserana: *Ceromya parviseta*, *Compsilura concinnata*.

Merophyas divulsana: *Voriella uniseta*.

PSYCHIDAE

Hylarcta huebneri: *Eozenillia remota*.

H. nigrescens: *Eozenillia remota*, *Exorista psychidivora*.

Oiketicus elongatus: *Chlorogastropsis orga*.

Psychidae: *Palexorista* sp.

PARASITISM BY THE FAMILY TACHINIDAE

OECOPHORIDAE

- Garrha hemiteles:** *Teretrophora fasciata*, *Trigonospila brevifascies*.
Philobota fascialis: *Teretrophora fasciata*.

XYLORYCTIDAE

- Areostoma aenicta:** *Chlorogastropsis* sp.

COPROMORPHIDAE

- Copromorpha prasinichroa:** *Peribaea argentifrons*.

LIMACODIDAE

- Doratifera casta:** *Austrophorocera* sp. nr. *grandis*.
D. ?quadriguttata: *Austrophorocera grandis*.
D. vulnerans: *Austrophorocera grandis*, *Compsilura concinnata*.
Doratifera sp: *Austrophorocera* sp., *Palexorista macquarti*.

PYRALIDAE

- Archernis mitis:** *Palexorista* sp.
Hymenia recurvalis: *Sisyropa* sp.
Loxostege affinitalis: *Stomatomyia tricholygoides*.

PAPILIONIDAE

- Graphium sarpedon choredon:** *Blepharipa* sp. *sugens* group.
Papilio aegeus aegeus: *Blepharipa fulviventris*, *Blepharipa* sp. 2.

PIERIDAE

- Artogeia rapae:** *Compsilura concinnata*.
Delias aganippe: *Carcelia* sp. 2, *Paradrino laevicula*, *Winthemia neowinthemoides*.

NYMPHALIDAE

- Danaus plexippus plexippus:** *Sturmia convergens*, *Winthemia neowinthemoides*.
Euploea core corinna: *Winthemia neowinthemoides*.

LASIOCAMPIDAE

- Digglesia australasiae:** *Palexorista* sp. nr. *macquarti*.

ANTHELIDAE

- Anthela acuta:** *Blepharipa* sp. nr. *fulviventris*, gen. nr. *Pareupogona*.
A. ariprepes: *Eozenillia remota*.
A. varia: *Carcelia murina*.
Anthela sp.: *Carcelia murina*.
?Anthela sp.: *Peribaea plebeia*.
Anthelid larva: *Austrophorocera* sp. 2.

EUPTEROTIDAE

Panacela lewinae: *Anamastax* sp. nov., *Carcelimyia dispar*; *Elpe* sp.

SPHINGIDAE

Psilogramma menephron: *Zygobothria atropivora*.

Theretra nessus: *Blepharipa fulviventris*.

Sphingidae: *Palexorista* sp. nr. *macquarti*; *Palexorista* sp.

NOTODONTIDAE

Teara contraria: *Exorista psychidivora*.

LYMANTRIIDAE

Leptocneria reducta: *Winthemia neowinthemoides*.

Teia anartoides: *Blepharipa* sp. 1; *Carcelia* sp. 3.

AMATIDAE

Amata sp. ?xanthura: *Stomatomyia tricholygoides*.

NOLIDAE

Uraba lugens: *Exorista flaviceps*.

NOCTUIDAE

Agrotis infusa: *Chaetophthalmus bicolor*; *Tritaxys milias*.

A. munda: *Chaetophthalmus bicolor*.

Agrotis sp.: *Tritaxys scutellata*, *Winthemia lateralis*.

Chrysodeixis argentifera: *Voria ruralis*.

Heliothis punctigera: *Chaetophthalmus biseriatus*, *Exorista currei*.

Heliothis sp.: *Carcelia illota*, *Chaetophthalmus biseriatus*.

Mythimna convecta: *Ceromya norma*, *Chaetophthalmus biseriatus*, *Microtropesa flaviventris*; *Palexorista* sp.; *Stomatomyia tricholygoides*; *Tritaxys scutellata*; *Winthemia lateralis*; *W. neowinthemoides*.

Neocleptria punctifera: *Goniophthalmus rufescens*.

Persectania ewingii: *Chaetophthalmus biseriatus*, *Microtropesa flaviventris*, *Tritaxys milias*.

Spodoptera exempta: *Exorista sorbillans*; *Goniophthalmus australis*; *Palexorista* sp.; *Stomatomyia tricholygoides*.

Noctuidae: *Palexorista* sp.; *Tritaxys milias*.

Armyworm: *Compsilura concinnata*.

AGARISTIDAE

Phalaenoides glycine: *Exorista psychidivora*.

PARASITISM BY THE FAMILY TACHINIDAE

HYMENOPTERA

PERGIDAE

Perga sp: ?*Austrophyrno* sp.

VESPIDAE

Polistes tasmaniensis: *Anacamptomyia nigriventris*.

Polistes sp. (nest): *Anacamptomyia nigriventris*.

DISCUSSION

Since it has not always been possible to identify either the tachinid or the host to specific level, some of the numerical data have to be regarded as approximate. Also in a few cases some of the locality records are indefinite, e.g. where New South Wales is given.

Four tachinid subfamilies were recognised by Crosskey (1973): Phasiinae, Proseninae, Tachininae and Goniinae. Members of the latter subfamily occur most frequently in the data recorded for the various insect orders.

HOST RELATIONSHIPS

MANTODEA. The only recorded species, *Exorista coras*, is one of the Goniinae.

ORTHOPTERA. *Ceracia fergusoni*, the only species mentioned here, is also a member of the Goniinae.

HEMIPTERA. *Alophora lepidofera* and *Leucostoma simplex* belong to the Phasiinae.

COLEOPTERA Scarabaeidae: of the three genera involved, *Senostoma* is one of the Proseninae, the other two being Tachininae. Chrysomelidae: the three genera having relevance are Goniinae (Blondeliini). Curculionidae: one species is a member of the Goniinae, the other of the Tachininae.

LEPIDOPTERA. In this order only four genera (*Chaetophthalmus*, *Voria*, *Microtropesa* and *Elpe*) belong to the Tachininae, the other 27 genera are Goniinae.

In the records quoted above, tachinids have, with one exception, attacked only one order of insects. However T.V. Bourke bred a specimen of *Chaetophthalmus bicolor* from the scarab *Sericesthis geminata*, while all other records of the genus are from Noctuidae. On this subject Cantrell (pers. comm.) has commented: "It cannot be absolutely ruled out as an incorrect record as tachinids sometimes "make a mistake" and attack a "wrong" host, yet are able to successfully complete development. The occasional rearing of *Exorista* spp. from mantids and tettigoniid grasshoppers are good examples.the record needs to be confirmed and should be treated with caution."

REGIONAL DISTRIBUTION

The Commonwealth Bureau of Meteorology divides the State into four regions. The distribution of bred flies in these areas is as follows: Coast 119 occurrences, from 65 localities; Tablelands 12 and 17; Western Slopes 9 and 17; Western Plains 18 and 26 respectively. Data on species are very often confined to one record and obviously cannot be regarded as final.

Two species, *Eozenillia remota* and *Tritaxys milias*, have been found in the four climatic areas of the State. *Stomatomyia tricholygoides* has not been noted from the Tablelands, but occurs in the other three regions, and *Tritaxys heterocera* is missing from the Western Plains only.

The following species are noted from two regions: *Anacomptomyia nigriventris* and *Microtropesa flaviventris* Coast and Western Slopes; *Ceromya norma*, *Medinodexia morgani* and *Voria ruralis*, Coast and Western Plains; *Carcelia murina*, Tablelands and Western Plains.

Six species are noted from the Coast only: *Austrophorocera grandis* (2 records), *Blepharipa fulviventris* (3), *Chlorogastropsis orga* (7), *Compsilura concinnata* (4), *Goniophthalmus australis* (2), and *Winthemia winthemoides* (6).

MONTHLY DISTRIBUTION

Emergences have been recorded in all months with an expected falling off in the cooler months as indicated by the following data: January (20 emergences), February (15), March (22), April (18), May (10), June (8), July (8), August (3), September (14), October (20), November (17) and December (20).

A number of factors influence records of geographic and seasonal distribution and any information on this subject reflects the information available at the time the study is made. Naturally future investigators with fuller data may indicate a need to modify present views on the subject, for example where a species is recorded from the Coast and Western Plains it would cause no surprise if it also occurs in the two intervening regions.

ACKNOWLEDGEMENTS

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Diving and Amphibious Behaviour in a Free-living *Crocodylus porosus*

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ABSTRACT

Twelve Estuarine Crocodiles (6-51 kg) were fitted with recording back packs in order to study the longevity, frequency and daily/tidal rhythm of natural dives by crocodiles free-living in their familiar habitat. Despite disinterest shown by captive crocodiles in removing their jackets in tank trials, all but one of the seven crocs recaptured 5-16 days after release had shed their jackets and recorders. Results from this 9.75 kg animal showed that it had a prolonged emergence during each daylight low tide (basking?), that it dived mainly in daylight hours (feeding?) predominantly in the upper half of the tide and that most dives were of very short duration (1-5 minutes). Even the longest dive, 30 minutes, was well within the aerobic capabilities of a crocodile this size. Although these results are from a single animal, and may turn out to be quite atypical, if attachment problems are solved the method has clear potential for revealing much about the daily activity patterns of free-ranging crocodiles, and other animals.

A study of diving behaviour in Estuarine Crocodiles, *Crocodylus porosus*, free-living in their familiar habitat was attempted in the Tomkinson River, northern Australia in October 1981 by fitting each of 12 crocodiles with a recording back pack. Information was collected from only one animal, but the experience gained would allow us to undertake a follow-up study with a much higher success rate. No opportunity exists for a follow-up study in the foreseeable future. Accordingly, we report here the data gained from that single animal, acknowledging whatever limitations it may have, in the belief that the results are of interest and may encourage others to employ similar techniques.

Questions, about the longevity, frequency and daily/tidal rhythm of natural dives in *C. porosus*, led us in 1979 to plan this study as background to laboratory studies of diving physiology in *C. porosus*. Meanwhile, the use of recording back-packs in free-ranging animals was applied with considerable success to Weddell seals (Kooyman *et al.* 1980), establishing that they typically dive repetitively and for only short periods when feeding under natural conditions.

Much has been written about terrestrial aquatic behaviour in various species of crocodilian, starting with Pliny who recorded that Nile crocodiles spend the day on shore and the night in the water, a view confirmed by Cott (1961). The importance of daytime shore basking has been drawn attention to by many authors. Little has, however, been recorded about diving patterns under natural conditions in any species, or about tidally correlated behaviour patterns in estuarine species. The main question we particularly wanted to address was whether on not dives too long to be accounted for by aerobic metabolism were common in *C. porosus*.

The recording unit was made by Kinney and Farwell (EnviRecord, Los Angeles). It was a battery-operated recording microprocessor sealed in a teflon casing (7.5 x 6.5 x 2.1 cm), with a spring-loaded insulated and hydrophobic probe attached to the brass lid of the unit. At the top of the probe was a gold-plated electrode. The probe was bent forward to cope with the *penchant* of crocodiles for resting in the water with the body sloping at approximately 45° (Fig. 1). The recorder was mounted on the crocodile in the pocket of a neutrally buoyant neoprene rubber jacket (Fig. 1). Trials with captive crocodiles had shown that this appeared not to prejudice their behaviour and that they did not attempt to remove it. The same trials showed also that all observed dives were recorded successfully. Each minute, the device sampled and recorded whether there was a conductive wet-bridge between the probe-tip and the lid of the casing. Any period of one minute or more was recorded as a dive, whereas

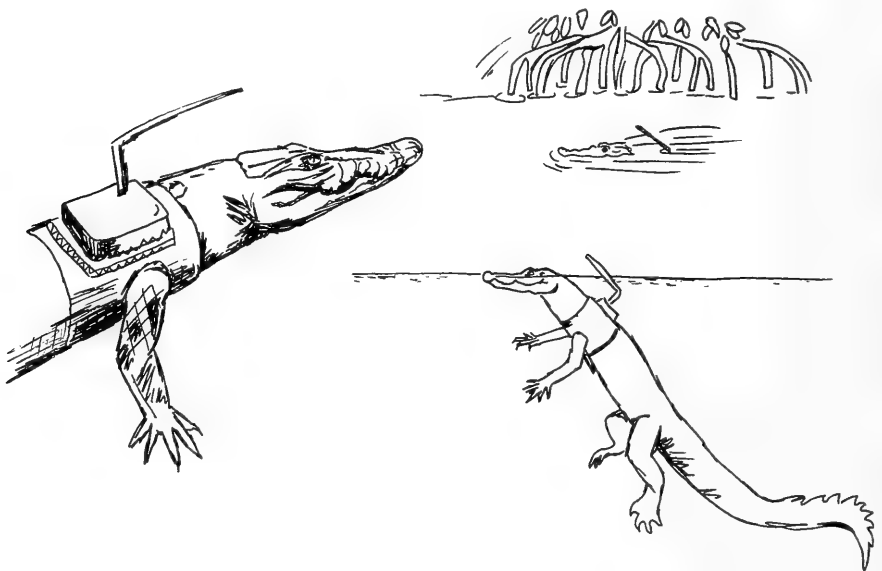


Fig. 1. Sketches of the crocodile and its recording back-pack.

ESTUARINE CROCODILE DIVING BEHAVIOUR

even a brief moment of surfacing during any one minute sampling period was not logged as a dive. Hence, the device was set-up to recognise brief surfacing between dives. While this missed very short dives, it avoided possible confusion from the lapping of waves over the probe tip. The recording unit could retain 8192 samples (thus total sampling time was 5.69 days). Sampling rate could be adjusted; the one minute rate was a compromise that missed very short dives but gave a reasonably long sampling time. Following recovery, the unit was interrogated with a read-out device activating a chart recorder (Figs 2, 3).

Crocodiles in the field study were caught by a non-injurious harpooning technique (Webb and Messel 1977). After being fitted with the recorder, each was released at its capture site in brackish or salt water between 17.2 and 54 km upstream from the open sea. Six of the jackets had a small radio-transmitter incorporated to aid relocation and recapture. A description of the habitat provided by the Tomkinson River (meandering, mangroved-fringed) may be found in Messel *et al.* (1979) and Grigg (1981). Contemporaneously, tritiated water and ^{22}Na were injected in order to study water and sodium fluxes (reported elsewhere, Grigg *et al.* submitted). Crocodiles were marked by scute-clipping. Seven of twelve crocodiles (65-122 cm SVL, 5.57-51.3 kg) were recaptured within 5-16 days, none more than 1500 m from the capture and release point. Despite the

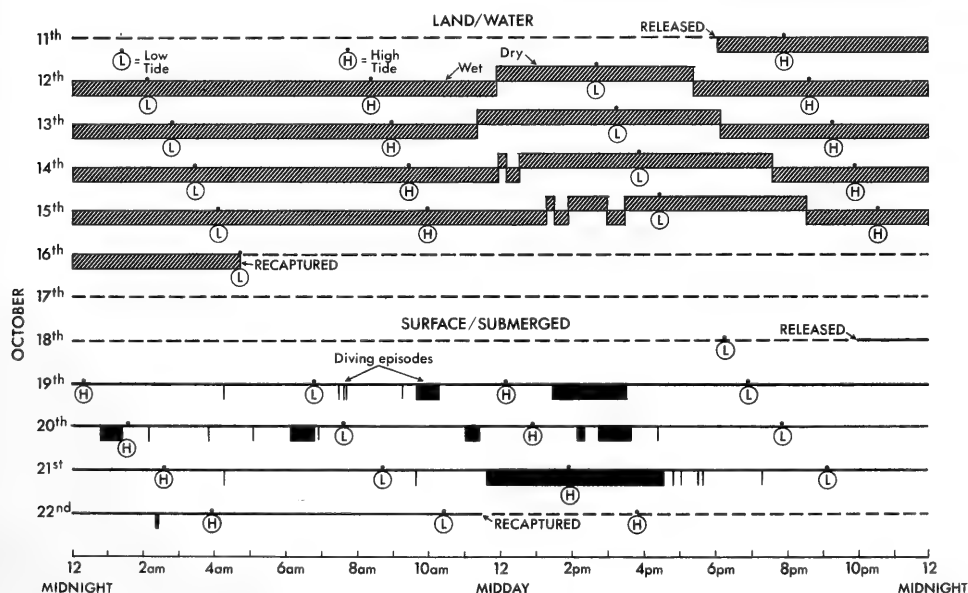
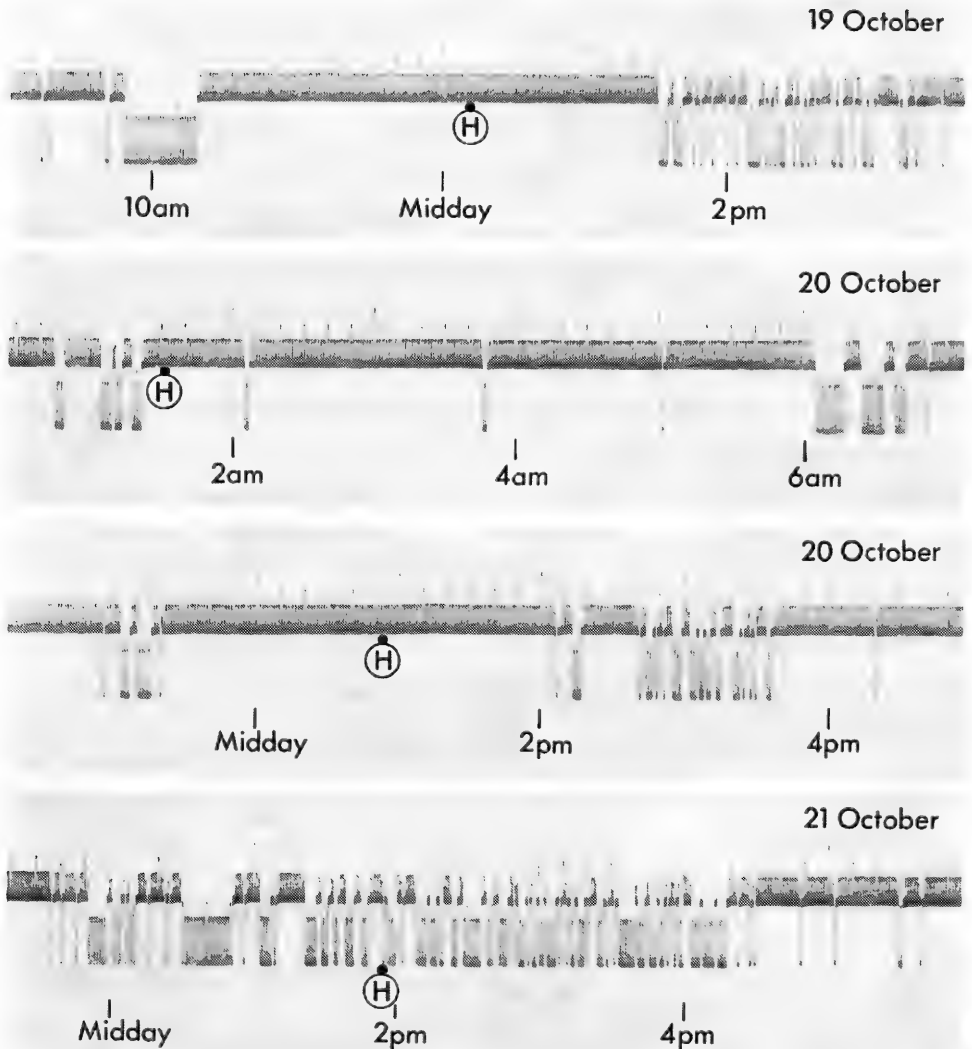


Fig. 2. Time spent by a 9.75kg female *Crocodylus porosus* on land and in the water (upper panel) October 11-14, and diving episodes (lower half) October 18-22, in the Tomkinson River, northern Australia, 1982. Circled H and L points mark times of high and low tide each day.



DETAIL OF MAJOR DIVING EPISODES

Fig. 3. Detail of read-out from the back-pack after recovery, showing a selection of the major diving episodes.

ESTUARINE CROCODILE DIVING BEHAVIOUR

disinterest shown by captive crocodiles in removing the jackets during diving trials, all but one (#2079) of the wild-ranging crocodiles had shed their recorders and back packs. Two abandoned recorders were recovered along the shore by radio-tracking but these yielded no unambiguous data.

The animal from which data were obtained successfully was a 9.7 kg (#2079) female captured 25.5 km upstream against the eastern bank and released at the same point at 1806 hrs Eastern Standard Time, October 11, 1981. She was recaptured at 0445 October 16. Interrogation of the recorder revealed that the probe had gained a thin film of river sediment which, when moist, allowed a conductive path from the probe tip to the metal lid of the recorder. Hence, the record did not show dive patterns, but whether the probe was wet or dry. This fortuitously gave useful information of a different kind (Fig. 2, upper half). The problem was rectified, the animal re-released at 2158 hrs, October 18 and recaptured at 1130 hrs October 22, whereupon it was found that the re-adjusted recorder had operated as planned (Fig. 2 lower half, Fig. 3).

The results show that this crocodile had a prolonged emergence during the daylight low tide (Fig. 2, upper). We interpret this to be time spent ashore.

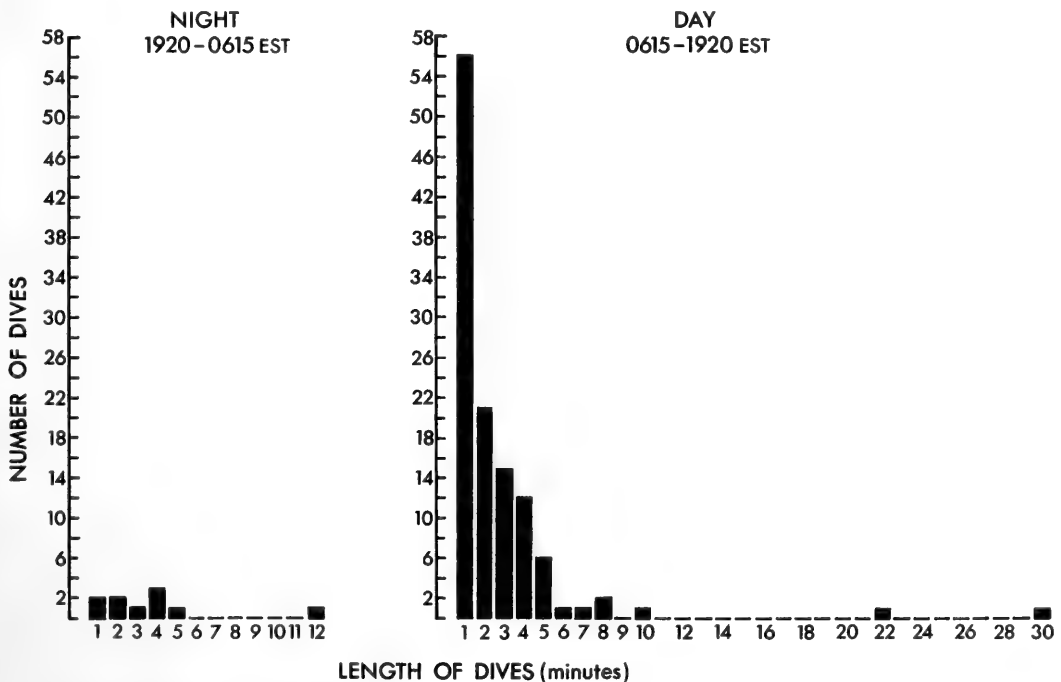


Fig. 4. Length/frequency distribution of dives one minute or longer, by night and by day, October 18-22, 1982.

Its periods of diving were mainly in daylight hours (Fig. 2, lower, Fig. 4), often (not always) associated with the upper half of the tide (Fig. 2, lower). The importance of the height of the tide as a determinant of behaviour is shown by middle-of-the-day time on land (basking?) on October 12, 13 at low tide, and middle-of-the-day diving (feeding?) on October 19, 20, 21. This interpretation predicts that the crocodile would likely be out of the water on the morning daylight low tides of October 20-22, about which we have no information from the dive recorder (except that there were no dives). However, her recapture followed our discovery of her right out of the water and up among the mangroves at about 10.30 a.m. October 22. Lack of up-directed tracks from the water's edge across the soft mud showed that she had been out of the water for some time. It seems likely that both time and tide are major factors influencing crocodile behaviour in tidal systems.

As to the length of dives, they are mostly very short (1-5 minutes) (Figs 3, 4) and have only brief intervals between, with, perhaps, only a single breath at the surface in many instances. The longest dive was 30 minutes, known to be well within the aerobic limit for a crocodile of that size (J. Wright, pers. comm.). Whether or not the periods of diving represent feeding periods is unknown, but probable. If they are feeding periods, then mainly daylight feeding seems reasonable for an animal with good visual skills but their pattern and duration (up to 5 hours) is inconsistent with the common perception of *C. porosus* as a sit-and-wait predator. An alternative hypothesis is that the periods of diving represent periods spent resting on the bottom in shallow water, as seen commonly in stressful situations in the laboratory, with surface visits to breathe. Such an interpretation is much less likely because of the irregularity of surfacing.

While no firm conclusions can be drawn from this preliminary study, it does enable some hypotheses to be advanced concerning the behaviour patterns of crocodiles under natural conditions. In any future study we would recommend a package that can monitor several types of information simultaneously (e.g. wet/dry, surface/dive, depth, temperature) as well as a larger memory so that a full tidal cycle could be recorded, as well as a reliable method of attachment to the animal. We think that this approach, with improving technology, shows a lot of promise for studies for free-living animals such as crocodiles which are so shy or cryptic in their natural habitat that direct observation without their being disturbed is almost impossible.

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The Australian Snapping Tortoise *Elseya latisternum*: A Successful Predator on the Introduced Cane Toad?

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Since its introduction into Australia in 1935 as an agent for the biological control of sugar cane pests (Mungomery 1935), the Cane Toad, *Bufo marinus*, has itself become a pest species (Cogger 1975, Tyler 1980). *B. marinus* has reached plague proportions in some areas of Queensland, and its range now extends from as far north as Weipa on the Cape York Peninsula (Hughes 1982) to the Byron Bay area of New South Wales (van Beurden and Grigg 1980). The species is also reported to have crossed the Queensland border into the Northern Territory during the 1982/83 wet season (Freeland 1984). Within its range, *B. marinus* occupies a wide variety of habitats and can breed successfully in almost any available source of standing fresh or brackish water (Covacevich and Archer 1975).

Although much of the general biological knowledge of the cane toad in Australia relies on anecdotal information, two well documented attributes of *B. marinus* have clearly contributed to its success. Firstly, the species is an indiscriminate feeder (see Tyler 1980 and Freeland 1984), supporting the belief that native frogs suffer in competition with it. Secondly, *B. marinus* is highly toxic (Meyer & Linde 1971) and can kill the endemic vertebrates that might otherwise contribute to its population control. Numerous respondents to a survey conducted by Easteal *et al.* (1984) noted a dramatic decline in the numbers of large predators such as varanid lizards and elapid snakes, following the spread of *B. marinus* into some areas. Earlier, Covacevich and Archer (1975) conducted a survey into the effects of cane toads on endemic vertebrates and established that members of at least twelve species (two species of birds, two of mammals, eight of reptiles) had died after mouthng or ingesting Cane Toads. In contrast, very few species have been shown to prey on *B. marinus*. Only *Amphiesma mairii* (common keelback snake) consistently eats live toads, though the observations of J. Covacevich (pers. comm.) suggest that the snake may be susceptible to the toxins of a full-grown adult toad. Of other vertebrate species known to eat cane toads occasionally, most seem to eat juvenile toads

(e.g. the Cattle Egret, *Ardeola ibis* — D. Seaton, pers. comm.), selected parts of the toad such as the tongue and intestines (e.g. the Water Rat, *Hydromys chrysogaster* — Covacevich and Archer 1975), or scavenge on already dead animals (e.g. *Corvus* sp. — Covacevich and Archer 1975). We wish to report here that an Australian freshwater tortoise, *Elseya latisternum*, appears to be a successful predator on *B. marinus*, and as such can be added to the very short list of vertebrate animals, in Australia and elsewhere, that feed on the Cane Toad with impunity. *El. latisternum* is a robust tortoise with a relatively large head and powerful jaws. It is primarily carnivorous (Legler and Cann 1980) and is known to eat frogs readily in captivity (Goode 1967).

Initial indications of *El. latisternum*'s resistance to Cane Toad toxin emerged during a comparative study of the diets of this and another freshwater tortoise, *Emydura signata*. Stomach contents of 232 specimens of *Em. signata* and 34 specimens of *El. latisternum* (captured in the Brisbane and South-Pine Rivers of south-east Queensland) were removed by a flushing technique. A steady flow of water provided by a 12-volt bilge pump was directed through a flexible tube into the tortoise's stomach. The water returned through the oesophagus carrying with it the items of food (after Legler 1977). Whereas none of the omnivorous *Em. signata* was found to have fed on cane toads, toad remains were recovered from the stomachs of four *El. latisternum*. The remains of toad limbs were recovered from the stomachs of three of these tortoises which were captured in the South-Pine River in September and October. The fourth tortoise, captured in the Brisbane River in October, had eaten a large piece of toad skin with both parotoid glands attached. The size of the toad remains indicated that all four tortoises had eaten parts, at least, of adult toads.

To determine whether the tortoises were preying on live toads, or scavenging on the remains of dead ones, we set up feeding trials and tested the responses of a further four *El. latisternum* to live toads, dead toads, toadlets and tadpoles. The tortoises were housed individually in glass aquaria, and water temperature was maintained at 25-26°C under a natural light regime. Specimens of *B. marinus* were collected from St Lucia, Brisbane, and were all active and apparently healthy. During the feeding trials, the tortoises were offered *B. marinus* as items of food in various forms:

- pieces of flesh and skin
- dead toads, bisected sagittally
- parotoid glands
- whole live toads
- live tadpoles

Each food item was weighed (± 0.1 g) before being used in a trial, as were any fragments that remained at the end of a trial, so that the weight of ingested food could be determined. The initial reactions of the tortoises to the food and

SNAPPING TORTOISE PREDATION ON CANE TOAD

their subsequent feeding behaviour, were recorded. After feeding, the tortoises were watched closely for signs of ill-effects.

During the feeding trials three *El. latisternum* were offered and ate *B. marinus* tadpoles, and all four ate live toadlets and various amounts of toad pieces, including parotoid glands, when these were placed in their aquaria. The two most voracious tortoises survived for periods of five and a half months and four months, respectively, on a diet of fresh toad alone (144 g and 267 g respectively). These two tortoises readily attacked and eventually ate live adult Cane Toads but the remaining two tortoises showed no apparent interest in live toads left in their respective aquaria for 10 days. None of the *El. latisternum* tested exhibited any ill-effects from ingestion of *B. marinus* and all were released in an apparently healthy condition.

The finding of Cane Toad remains in the stomachs of some *El. latisternum* in the field, combined with the tortoises' demonstrated abilities to prey on live adult toads, toadlets and tadpoles in the laboratory, leaves little doubt that the species is resistant to *Bufo* toxins and has the capacity to be a successful predator of all active stages of the life cycle of *B. marinus*. The most recent estimates of *El. latisternum*'s range (Legler 1981) show it to be roughly coincident with that of the toad (Easteal *et al.* 1984), allowing considerable opportunity for *Bufo* predation by the tortoise.

Resistance to toad toxin is unusual in vertebrates, with the result that adult toads have few natural predators apart from some toad-eating snakes such as *Thamnophis* (Fitch 1941), *Heterodon* (Edgren 1955) and *Natrix* (Bowers 1966). None of these genera occurs in Australia, and all may have co-evolved with various *Bufo* species. In contrast, Australian freshwater tortoises have had contact with *B. marinus* only since the toad's introduction to Australia, so that apparent resistance to toad toxin in *El. latisternum* is somewhat surprising. At present, the levels of resistance to toad toxin exhibited by these tortoises are not known; nor do we understand the mechanisms by which they cope with ingestion of the toxins. Possible mechanisms for resistance to toad toxin in *Thamnophis* and other toad-eaters have been discussed briefly by Licht & Low (1968). They suggested that the cardiac tissue of the predators may have become adapted to resist the many cardio-active components of toad toxin, or alternatively that the gastro-intestinal mucosa of toad-eaters may prevent absorption of the toxins when they are in low concentrations. They further proposed that the buccal mucosa of the predator may be adapted to withstand the harsh burning effects suffered by mammals on contact with the toxin. Other studies (Smith and White 1955) have indicated that the adrenals may function to confer resistance to toad toxins. The results of the present study indicate that *El. latisternum* might prove a good subject for further investigations into the nature of resistance to the toxins of *B. marinus*.

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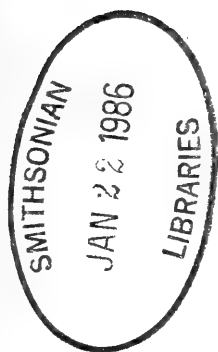
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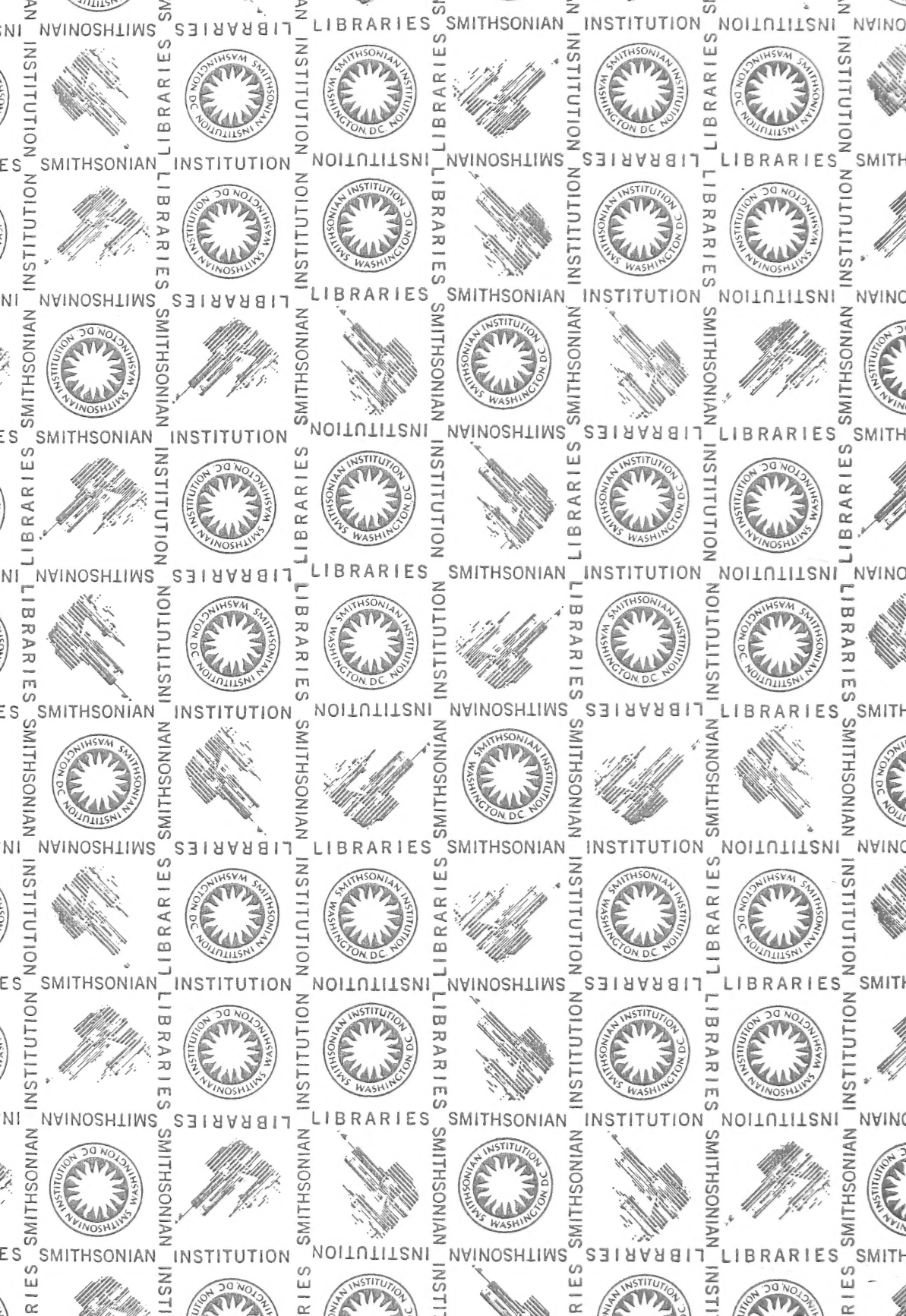
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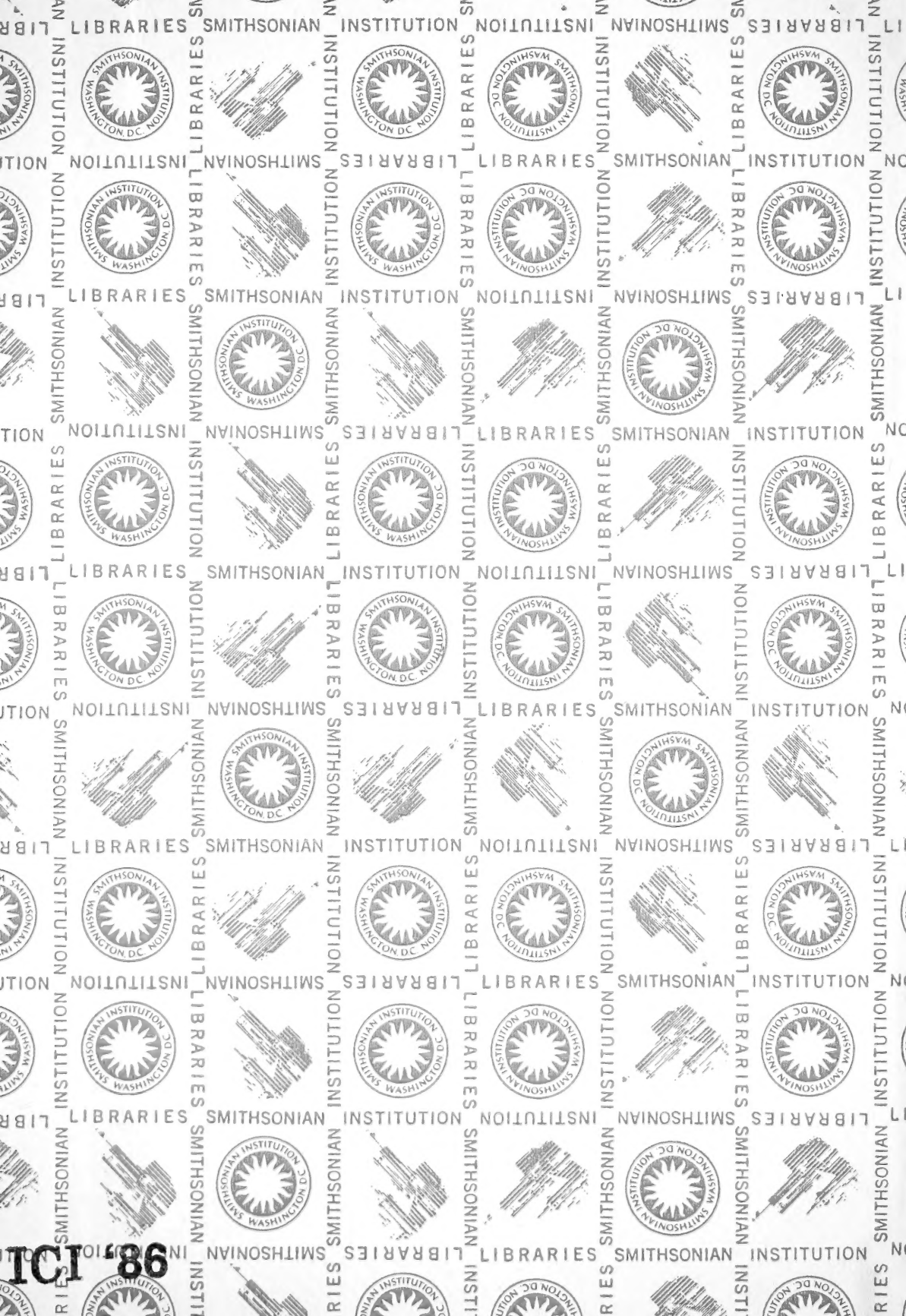
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